The lives and times of jellyfish: Modelling the population dynamics and ecological role of jellyfish in marine pelagic ecosystems

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Ph.D. thesis

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August 2017

DTU Aqua
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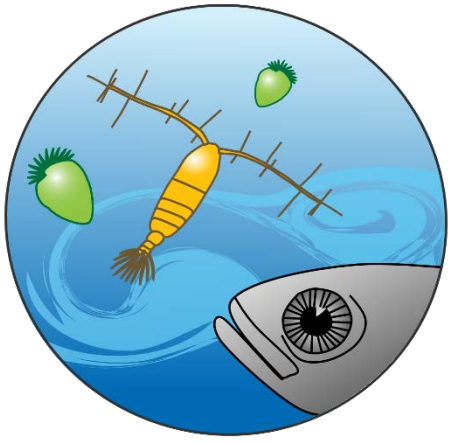

Centre for Ocean Life
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Preface

This thesis is the culmination of three years of research, and is submitted as part of the requirements for obtaining the Doctor of Philosophy degree (Ph.D.) at the Technical University of Denmark (DTU). The research was carried out from August 2014 until August 2017 at the Centre for Ocean Life, a Villum Foundation Centre of Excellence at the National Institute of Aquatic Resources (DTU Aqua) in Charlottenlund and Lyngby, and at the Max Planck Institute for the Physics of Complex Systems in Dresden Germany. During these three years, I was supervised by Senior Researcher Dr. Patrizio Mariani as well as by Professor Dr. Thomas Kiørboe. During my stay in Dresden, I was supervised by Professor Dr. Simone Pigolotti, then a guest scientist at the institute.

Through the Centre for Ocean Life, my Ph.D. project was funded by the Villum Foundation, and two travel grants from the Otto Mønsted Foundation supported conference participation in Waterville Valley, New Hampshire, and Barcelona, Spain.

The image on the front page shows a jellyfish bloom, revealed by the flash of a nightly photographer, with Århus harbor looming in the background. The image is a nice metaphor for the research of jellyfish – the flashlight of science illuminates the dark ocean, and reveals its inhabitants in all their strange and disturbing beauty, while the activities of man looms in the background. Do the jellyfish threaten the world of man, or is it the other way around? My thanks go to Casper Tybjerg, professional wildlife photographer, who was kind enough to let me use the image.

Acknowledgements

I am grateful to a great many people, without whose company, this thesis would not have been possible. I am deeply grateful to the leadership at the Centre for Ocean Life, for giving me the opportunity to pursue this thesis, and to Ken Haste Andersen for inspiring me to apply in the first place. Most importantly however, I would like to thank my main supervisor Patrizio Mariani, who has helped and supported me in the last three years. While we have not always initially agreed, we have always had very fruitful interactions, and his resourcefulness, great competence and enthusiasm (and gentle prodding when needed) has kept me on track these last few years. I have learned a great deal from him, not least of which is the immensely useful skill of how to open a bottle of wine with nothing more than a shoe and an old torpedo. I would also like to thank my second supervisor Thomas Kiørboe, whose keen eye for the weaknesses in any scientific work, and somewhat direct, but nonetheless encouraging nature has been a refreshing touch, that has sometimes saved me a lot of time. My thanks also go to Simone Pigolotti, who provided useful advice and comments on my first project at a crucial stage, and became a collaborator on my third project, where I continue to enjoy our interactions. I thank the Max Planck Institute for the Physics of Complex Systems for being gracious enough to host me, even though I was only visiting their visitor.

These three years would have been a lot duller without the many wonderful people at the Centre for Ocean Life. I have enjoyed interacting with everyone there, and cannot imagine a more inspiring and pleasant workplace. Special thanks go to Phillipp Brun and Kasia Kenitz for sharing the best office in Maskinhuset with me, I will remember our many laughs and discussions with fondness, even the work-related ones. I also thank Hans van Someren Gréve for being a brother-in-arms on the arrangement of many an event, both social and work-related. May we both one day master the task of assessing the appropriate amount of drinks to buy.

Of course, one cannot talk about the last few years, without mentioning the coffee room. Mushroom farms, couch discussions, coffee buying schedule, the Dutch Mafia office gossip and a notice board filled with nerdy cartoons. I thank Laurène Pécuchet for being an original co-conspirator for purchasing our beloved coffee machine, and Thomas Kiørboe for providing indirect financial support, a decision I am sure he has regretted ever since.

I would also like to thank Müsli from Costa Smeralda, whose many greasy, but delicious sandwiches have kept my body oiled and running on many a good, long workday.

Finally, I would like to thank my loving wife Fie, as well as the rest of the family for their continued support and always at least somewhat enthusiastic ears. You guys are my past, present and future and I love all of you.

Summary

Jellyfish are found nearly everywhere in marine environments, and have existed virtually unchanged for more than 500 million years. Jellyfish are often considered marine 'pests', as they form large, unpredictable blooms that inconvenience human activities, but despite this, they have historically been largely ignored in marine science. Recently, interest in jellyfish ecology has picked up due to the widespread and increasing human impact on the marine environment that have in many cases benefited jellyfish. However, the study of jellyfish and their role in marine ecosystems is hampered by a lack of data, and the use of theoretical models to investigate jellyfish population dynamics is a promising tool for increasing our knowledge of these fascinating animals.

Jellyfish share many common traits that set them apart from other organisms, such as their inflated and simple body plans, fast growth rates and reproduction, efficient swimming and feeding, and high clearance rates. In this thesis, we theoretically investigated characteristic traits of jellyfish, and how they can contribute to the patterns of jellyfish occurrence in the world's oceans and the ability to form blooms. The thesis is based on three studies that are quite different, but each focused on an important aspect of jellyfish ecology, with emphasis on how traits of jellyfish interact with the environment to regulate jellyfish population dynamics.

All jellyfish are tactile predators that rely on direct contact with their prey in order to catch it. This contrasts with the visual feeding of their main competitors, i.e. zooplanktivorous forage fish. In the first study of this thesis, we examined the competition between forage fish and large zooplanktivorous jellyfish in a global context, as influenced by water clarity and fishing. The contrasting feeding traits between the two groups causes jellyfish to have an advantage over fish in unclear water, because they are not dependent on sight to catch their prey. Using a simple food web model with mechanistic descriptions of feeding processes, we showed that this difference may explain much of the global patterns of jellyfish occurrences.

In spite of their similarities, different jellyfish can have fundamental differences in key traits, such as feeding mode and life cycle. In the second study, we investigated the interactions between environmental variation and jellyfish life cycles. The aim was to explore how environmental variation can contribute to the fluctuating nature of jellyfish populations, and how the two fundamental life cycles of jellyfish could be expected to respond to different environmental variations. We found that observed patterns of jellyfish blooms can indeed be explained by different types of variation, and predicted different responses of the two main jellyfish life cycles to seasonality and other key environmental factors.

The third study was dedicated to the important, but understudied polyps of scyphozoan jellyfish, and their complex asexual reproductive biology. Using an evolutionary model, we investigated the allocation of resources into three basic modes of reproduction in jellyfish polyps; fast local reproduction, dormant and mortality-resistant cyst production and dispersing motile buds. Consistent with observations, our evolutionary model predicted the evolution of more than one strategy in most cases, and we predicted how each strategy should be favored by different environmental effects.

Jellyfish are underrepresented in ecosystem models, and there is therefore a drive to better understand and describe jellyfish population dynamics. The lack of good data on jellyfish populations provides an opportunity to form our understanding of the roles of jellyfish in marine systems from the 'bottom up', constructing mechanistic descriptions of the key traits and features that sets jellyfish apart, and then comparing the predicted dynamics to the data and observations that are available. Such models can help piece together the key interactions for developing predictive capabilities when it comes to jellyfish populations. The three studies in this thesis represent different approaches and scales of models, and provide examples of how theoretical mathematical models are a flexible tool than can be tailored to specific situations and questions. However, they also highlight the need for more field studies, in order to validate the predictions of models. Developing our understanding of how understudied, but important, groups like jellyfish fit into marine ecosystems, and how they depend on environmental conditions, is a pressing task, as human pressures on the marine environment are only expected to increase in the future.

Dansk resumé

Gopler er udbredte i alle verdens marine miljøer, og er stort set uændrede siden deres opdukken for mere end 500 milioner år siden. Gopler bliver ofte anset for skadelige for de marine økosystemer, da de kan danne store og uforudsigelige opblomstringer, med skadevirkninger for menneskelige aktiviteter, men på trods af dette er de historisk set ofte blevet ignoreret i den marine forskning. Interessen for goplers økologi er dog den seneste tid øget, på grund af de store og stigende menneskelige påvirkninger i det marine miljø, som i mange tilfælde har været til gavn for goplerne. Studiet af gopler og deres rolle i de marine økosystemer bliver ofte besværliggjort af manglen på data, og brugen af theoretiske modeller til at undersøge goplepopulationer er derfor et lovende redskab til at øge vores viden om disse fascinerende dyr.

Gopler deler en række træk som adskiller dem fra andre organismer, såsom deres 'oppustede' og simple kroppe, hurtige vækstrater og reproduktion, og effektive svømning, fødeindtag og -søgning. I denne afhandling undersøger vi karakteristiske træk ved gopler teoretisk, og specielt hvordan de bidrager til goplers observerede globale udbredelsesmønstre og evne til at danne opblomstringer. Afhandlingen er baseret på tre forskellige studier, som alle fokuserer på et vigtigt aspekt af goplers økologi, med fokus på hvordan deres træk interagerer med miljøet og regulerer deres populationsdynamikker.

Alle gopler er taktile predatorer, som afhænger af direkte kontakt med deres bytte for at fange det. Dette kontrasterer med fødesøgningen hos deres primære konkurenter, zooplanktivore fisk, som bruger synet til at lokalisere byttet. I det første studie i denne afhandling undersøger vi konkurrencen mellem fisk og gopler i en global kontekst, under indflydelse af sigtbarhed og fiskeritryk. De kontrasterende fødesøgningstræk mellem de to grupper betyder at gopler har en fordel i forhold til fiskene, når vandet er uklart, fordi de ikke er afhængige af at se byttet. Ved hjælp af en simpel fødenet-model med mekanistiske beskrivelser af fødesøgningen viser vi at denne forskel kan forklare en stor del af de globale mønstre i gobleforekomster.

På trods af deres mange ligheder, er der også grundlæggende forskelle i nøgletræk mellem forskellige gopler, især når det kommer til fødesøgning og livscyklus. I det andet studie undersøgte vi interaktioner mellem møljøvariation og goplers livscyklus. Formålet var at udforske hvordan mljøvariation kan bidrage til goplepopulationers flukturerende natur, og hvordan de to fundamentale livcyklusser som findes blandt gopler kan forventes at reagere på forskellige mljøvariationer. Vi fandt at observerede mønstre i gopleopblomstringer kan forklares af forskellige typer af variation, og forudsagde at de to primære livscyklusser i forskellig grad afhænger af sæsonintensitet og andre miljøfaktorer.

Det sidste studie var dedikeret til scyphozore goplers vigtige, men underbelyste, polypstadie, og deres komplekse asexually reproduktion. Ved hjælp af en evolutionær model undersøgte vi allokeringen af resourcer til tre grundlæggende formeringstyper i goplepolypper; hurtig lokal reproduktion, produktion af hårdføre hvilecyster, og knobskydning af mobile partikler. I overensstemmelse med observationer forudsagde vores evolutionære model at flere strategier oftest blev selekteret, og vi forudsagde hvordan de tre strategiers selektion bør afhænge af forskellige miljøfaktorer.

Gopler er underræprensenterede i økosystem-modeller, og der er derfor behov for en bedre forståelse og beskrivelse af deres populationsdynamikker. Manglen på gode data om goplepopulationer betyder dog også at der er en mulighed for at forme vores forståelse af goplers rolle i de marine systemer fra bunden og op, ved at konstruere mekanistiske beskrivelser af de nøgletræk og karakterer som er unikke for gopler, og derefter sammenligne derved opnåede forudsigelser med de tilgængelige observationer. Sådanne modeller kan hjælpe med at stykke de afgørende interaktioner der er nødvendige for at kunne beskrive goplepopulationers dynamik sammen. De tre studier i denne afhandling repræsenterer forskellige tilgange til modellering, og giver eksempel på hvordan teoretiske matematiske modeller er et fleksibelt redskab der kan tilpasses den konkrete situation eller spørgsmål. Udover dette under streger de dog også behovet for flere feltstudier, hvis resultater kan danne sammenligningsgrundlag for modellernes forudsigelser. At udvikle vores forståelse af hvordan underbelyste, men vigtige, grupper som gopler passer ind i marine øosystemer, og hvordan de afhænger af miljøetbetingelserne, er en presserende opgave på grund af de menneskelige påvirkninger af verdenhavene; påvirkninger som kun forventes at øges i fremtiden.

Image credits

Front page photo and Figure 2: *Samling af vandmænd fotograpeheret ud for Århus havn, der ses i baggrunden*. Copyright belong to Casper Tybjerg (http://www.ttfoto.dk/). Reprinted with permission.

Figure 4: Jellyfish photo *ghost*. Copyright belong to fPat Murray on flickr.com (https://www.flickr.com/photos/fpat/). Image use licensed under creative commons (CC BY-NC-SA 2.0).

Figure 5: *Eastern Bering Sea Ecopath food web*. Reprinted from Deep-Sea Research Part II: Topical Studies in Oceanography, Vol 54, Aydin, Kerim and Mueter, Franz, The Bering Sea—A dynamic food web perspective, Page 2507, Copyright (2007), with permission from Elsevier.

Title page figure for Manuscript 1: Copepod drawing by Hans van Someren Gréve. reprinted with permission.

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Contents

Chapter 1. **Introduction**

1.1 Jellyfish Ecology

1.1.1 What are Jellyfish?

While it may seem a trivial question, defining the meaning of the term 'jellyfish' at the beginning of this thesis is important, because so many different definitions of this term are in use in the scientific literature. Some authors (e.g. Brotz et al. 2012) use the term as a catch-all phrase that is synonymous with gelatinous zooplankton of all types, i.e. mainly cnidarian medusae, ctenophores and pelagic tunicates, whereas others insist on restricting the term to mean cnidarian medusae only (e.g. Purcell 2012). Some scientist even argue that the word jellyfish should not be used at all, because jellyfish are not 'fish', in an evolutionary or taxonomic sense. However, most often (e.g. Pitt et al. 2013) the term is used as referring to all pelagic cnidarians and ctenophores (see figure 1), since, even though this grouping is polyphyletic and the two groups belong to separate phyla, they share several important traits, have similar ecological niches and habitats, and similar impacts on human activities. Unless otherwise stated, this is the definition of the word that will be used throughout this thesis.

Figure 1. Examples of jellyfish. Left: Among jellyfish, the closely related members of the genus Aurelia ***are probably simultaneously the most well-studied, most cosmopolitan, and most frequently blooming jellyfish in the world. Right:*** Mnemiopsis leidyi ***is a lobate ctenophore. Native to the east coast of north America, this species has invaded many coastal seas around the world, most notably in the Black Sea, where it was involved in a series of major ecosystem regime shift in the late 20th century.***

Whether cnidarian or ctenophore, jellyfish are characterized by having relatively simple body plans consisting of an epidermis and an endodermis with a gelatinous mesoglea in between. This mesoglea consists of an extracellular matrix of mostly water and collagen, and provides the bulk of the mass of an individual, resulting in a very high overall water content (>95 %) of the jellyfish. This high water content 'inflates' the animal, so that it has a larger size compared to other animals of similar carbon content, which gives it several advantages, including high clearance rates (Acuña et al. 2011), Reynolds numbers, and growth rates (Pitt et al. 2013). However, the longevity of jellyfish does not increase with size as for other animal groups, and the large watery bodies of jellyfish are fragile and vulnerable to physical stress and parasite infection, and causes jellyfish to be relatively slow swimmers for their size (Pitt et al. 2013). Additionally, the simple body plans do not allow for the storage of resources, so that jellyfish must instead shrink in response to starvation (Goldstein & Riisgård 2016).

In spite of their simple body plans, jellyfish are very successful animals. Both cnidarians and ctenophores are among the oldest multicellular animals on the planet, both groups going back more than 500 million years in the fossil record (Conway Morris & Collins 1996; Cartwright et al. 2007), and having changed very little since then. In the last 40-50 years, jellyfish have attracted increased attention both in the scientific community and the public eye, due to the ability of some jellyfish to form spectacular blooms. These blooms are mainly formed by cnidarians, predominantly members of the class scyphozoa (see table 1). As human activities in the oceans have increased, these blooms increasingly interfere with human interests, and often occur in areas that are heavily perturbed by human impacts, to the point that some authors have suggested that the world's oceans as a whole are moving towards an undesirable alternate state dominated by jellyfish instead of fish. Whereas it is debatable whether jellyfish populations are in fact increasing globally (Richardson et al. 2009; Brotz et al. 2012; Condon et al. 2012; Condon et al. 2013; Gibbons & Richardson 2013), understanding the biology of these organisms and the conditions that lead to blooms is important.

Table 1. Frequency of different jellyfish groups in coastal areas where blooms frequently occur (tallied on the basis of Graham et al. 2014, their WebTable 3).

Phylum	Class	Order	Genus	# of records	% of records
Cnidaria				216	85
	Scyphozoa			167	66
		Semeostomeae		104	41
			Aurelia sp.	55	22
		Rhizostomae		63	25
	Hydrozoa			32	13
	Other groups			19	7
Ctenophora				32	13
		Lobata		28	11
			Mnemiopsis leidyi	24	9
		Others		4	2
			Total # of records	254	100

*groups which almost exclusively include actively feeding jellyfish.

1.1.2 Jellyfish feeding and ecological roles

Almost all jellyfish are predators that rely on the capture of zooplankton prey (except some species of cnidarians which at least in part obtain their energy from photosynthesis by symbiotic zooxanthella). Jellyfish predators are dependent on direct contact with their prey in order to capture it and feed (Kiørboe 2011). Whereas many jellyfish have light-sensitive cells used for orientation and navigation, and some few even have highly developed eyes with lenses (Nilsson et al. 2005), they do not detect prey at a distance but are instead reliant on the prey coming into contact with tentacles or other capture surfaces, through the prey either swimming into them (passive ambush feeders) or being entrained in feeding currents created by the jellyfish (active feeders, see Costello & Colin 1995; Kiørboe 2011). Throughout this thesis, I will focus on actively feeding jellyfish, because it is predominantly this type of jellyfish that form blooms (Graham et al. 2014, table 1), and because the typically smaller ambush feeders have different ecological roles (Costello et al. 2008; Dawson & Hamner 2009).

Whether active or passive, jellyfish have specialized cells on their capture surfaces that are responsible for getting hold on the prey, but the exact method of capture differs between cnidarian and ctenophore jellyfish. Whereas most ctenophores use sticky cells called colloblasts to adhere to their prey, cnidarians use cnidocysts; specialized cells that on cue fire a long tubule into their prey, injecting them with venom. Thus, only cnidarian jellyfish are able to deliver painful stings.

Apart from the method of capture, jellyfish also differ in their mode of locomotion. Ctenophores have rows of cilia along their bodies (responsible for their other name 'comb jellies'), which beat in synchronization, while cnidarian medusae swim through the

contraction of their bells, pushing water backwards and propelling the animal forwards. While the locomotion of especially larger jellyfish is slow compared to similar-sized organisms, their cost of transport is among the lowest on the planet. In cnidarian jellyfish, this is due to passive energy recapture in the bell, and wake vortices which keep the animal moving, even when the bell is relaxing (McHenry & Jed 2003; Costello et al. 2008; Gemmell & Costello 2013). This allows even large (up to 2 meters in bell diameter) jellyfish like *Nemopilema nomurai* or *Cyanea capillata* to be efficient feeders and swimmers, despite being propelled exclusively by the contractions of a single epidermal layer of muscle fibers.

Jellyfish can be very efficient predators of zooplankton, and continuously swim through the water, straining it of prey. Many prey items can be handled at once, and the capacity for prey in the stomach is usually large. Because of these factors, the clearance rates of jellyfish are largely unaffected by (naturally occurring) prey concentrations (Bishop 1967; Clifford & Cargo 1978; Hansson & Kiørboe 2006; Møller & Riisgård 2007a). This lets jellyfish take advantage of periods of high food availability, which is part of the reason why jellyfish have very high maximum growth rates (Pitt et al. 2013). In general, actively feeding jellyfish are well adapted towards short pulses of abundant resources, having high reproductive output regardless of life cycle, rapid growth rates and high tolerance toward starvation (Hamner & Jenssen 1974). This fact, along with their generally short life spans, means that jellyfish tend to have periodic and highly variable population dynamics, often suddenly appearing in large numbers, only to later disappear (see figure 2). These jellyfish blooms are predominantly a coastal or shelf sea phenomenon (Brotz et al. 2012; Robinson et al. 2014) because these areas have high production to support blooms, and because most blooming jellyfish are dependent on suitable benthic substrate for their polyps (see the next section).

In large numbers, jellyfish can have a tremendous impact on local ecosystem structure, reducing zooplankton populations severely, and sometimes leading to phytoplankton blooms (e.g. Huntley & Hobson 1978; Møller & Riisgård 2007b; Tiselius & Møller 2017). Because jellyfish are dependent on the same zooplankton as the small planktivorous fish ('forage fish') that form the basis of many higher level food chains, jellyfish proliferations have often been connected to declining fish stocks (e.g. Oguz & Gilbert 2007; Dong et al. 2010; Roux et al. 2013; Robinson et al. 2014). However, though direct competition has often been inferred, it is difficult to prove, especially since jellyfish populations are often patchily distributed in both time and space.

Figure 2. A bloom of Moon jellyfish (*Aurelia aurita*) outside Århus harbour in Denmark.

For example, in the case of the Black Sea, where a decade-long population explosion of the invasive ctenophore *Mnemiopsis* coincided with a collapse in small pelagic anchovy, the question of causality, and especially whether the increase in *Mnemiopsis* populations was a cause or effect of the collapse, has been a subject of intense debate (Oguz et al. 2001; Daskalov 2002; Daskalov et al. 2007; Oguz & Gilbert 2007; Daskalov 2009; Llope et al. 2011). However it is clear that many human impacts that are harmful to fish stocks, such as fishing, eutrophication and oxygen depletion have less severe, neutral or even beneficial effects on jellyfish populations (Purcell 2012). The subject is further complicated by the fact that jellyfish are also often opportunistic predators of the early life stages of fish (Purcell & Arai 2001). Whereas jellyfish was previously thought to be a trophic 'dead end', except for a few specialized predators such as the sun fish *Mola mola* and leatherback turtle *Dermochelys coriacea* (see e.g. Lynam et al. 2006), recently it has been recognized that jellyfish are also routinely and opportunistically consumed by a large variety of fish species (Arai 2005; Cardona et al. 2012; Milisenda et al. 2014), although their pulsed occurrence and few specialized predators mean that they are probably rarely controlled by predation.

1.1.3 Jellyfish life cycles

Whereas jellyfish share some fundamental traits, one area where there are large differences is in life history. Roughly speaking, the most important division in life history occurs between ctenophores, which are holoplanctonic, and cnidarians, which are predominantly metagenic, having a benthic polyp stage and a pelagic medusa stage (figure 3). Ctenophores are hermaphroditic, and most species are thought to be self-fertilizing (Martindale & Henry 2015, see figure 3B). Eggs and sperm are produced internally and released into the water, were fertilization occurs. The fertilized eggs develop directly, and the juveniles of many species are themselves able to reproduce before maturity. Ctenophores are therefore able to increase their numbers very rapidly when prey is sufficiently available.

In contrast to the relative simplicity of the ctenophore life cycle, cnidarians have some of the most complex, diverse and plastic life cycles among animals (see figure 3A). While a few species are holoplanctonic, the life cycle of most species is separated into a small benthic, sometimes colonial, asexually reproducing polyp stage, and an adult, pelagic and sexually reproducing medusa stage (the jellyfish). Among cnidarian jellyfish, the highest life cycle diversity is within the hydrozoa, which includes examples of both holoplanctonic and purely benthic species in addition to the typical metagenic life cycle, as well as both colonial and solitary species. Among the scyphozoan cnidarians, which account for two thirds of coastal jellyfish blooms (table 1, figure 3A), the species are mostly metagenic and have a solitary benthic polyp (Dawson & Hamner 2009). These polyps produce small medusae (called ephyrae) through a special budding process called strobilation, either resulting in a single or multiple (tens of) ephyrae, and most polyps are, under ideal conditions, able to repeat this process several times in a season (Lucas et al. 2012). In addition to producing the adult generation, these benthic polyps are usually also capable of one or more modes of asexual reproduction resulting in additional benthic polyps. Thus, the potential production of adult medusae resulting from a single polyp can be very great, and benthic polyps are therefore thought to be important for the ability of many species to form sudden blooms (Dawson & Hamner 2009; Lucas et al. 2012; Schiariti et al. 2014), however, the combined dynamics of medusa and polyp populations have rarely been considered.

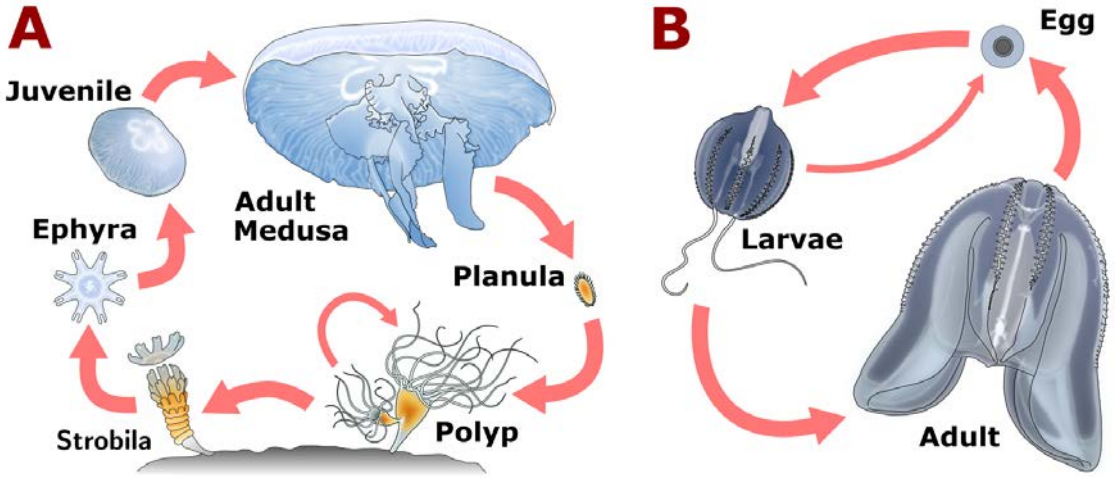

Figure 3. Illustration showing the typical life cycles of jellyfish. A) The metagenic life cycle of a typical scyphozoan jellyfish (here represented by* Aurelia *sp). The adult female jellyfish produces a planula larvae after being fertilized with sperm from a male, which settles as a polyp. The polyp can reproduce asexually, producing more polyps, but can also form a strobila to produce several larval jellyfish (ephyrae). The ephyrae grows and matures into an adult, restarting the cycle. B) The holoplanktonic life cycle of a lobate ctenophore. The adult jellyfish is hermaphroditic, and capable of self-fertilization. The resulting egg hatches into a larva, which can itself start to reproduce before reaching adulthood.

1.1.4 Jellyfish interactions with humans

Jellyfish provide several ecosystem services to humans (reviewed in Graham et al. 2014). First and foremost, jellyfish are a traditional source of food in East Asia, and support large fisheries there and in the Gulf of Mexico (Hsieh et al. 2001). Additionally, jellyfish can also locally be an important carbon sink, contributing to the global biological carbon pump (Sweetman & Chapman 2015). Recently, jellyfish have also become an attraction at public aquaria, and wild populations have also become a tourist attraction in certain areas of the world (Graham et al. 2014). Certain companies even offer lighted aqua with live jellyfish as 'jellyfish art' for indoor decoration (https://www.jellyfishart.com/). Finally, jellyfish are also a source of new compounds in medical research (Graham et al. 2014).

However, the negative consequences of jellyfish on human activities significantly outweighs the benefits as jellyfish populations increase (Graham et al. 2014). As previously stated, jellyfish may compete with more valuable forage fish species for resources, reducing the fish stocks available for fishing or for valuable higher trophic level predators. However, jellyfish also have more direct impacts on human activities (Graham et al. 2014). Interfering directly with fisheries, jellyfish can clog fishing nets, destroying the catch or nets and resulting in lost revenue or even fisheries closures. Jellyfish can also cause mortality in aquaculture and obstruct important human infrastructures like the water intakes of power plants. Finally, jellyfish can be detrimental for tourism, because of the risk of injury or death from jellyfish stings, and the resulting beach closures. Costs

result both directly from the deployment of protective measures and treatment, but also from lost revenue, as tourists redirect to other destinations.

With these adverse consequences of jellyfish proliferations in mind, it is of particular importance to identify how anthropogenic impacts on the marine environment can directly or indirectly alter jellyfish populations (recently reviewed in Purcell 2012). As already discussed, **overfishing** on forage fish stocks may release jellyfish from competition, and the regions where jellyfish often bloom almost completely overlap with the largest coastal fisheries in the world (Graham et al. 2014).

Eutrophication is another process that may benefit jellyfish both directly and indirectly. First and foremost, eutrophication leads to increased production, resulting in more food for jellyfish, but it may also change the competitive balance between jellyfish and their forage fish competitors, because increased phytoplankton densities lead to increased water turbidity, which affects the predominantly visual fish negatively, but not the tactile jellyfish (Eiane et al. 1997; Eiane et al. 1999; Sørnes & Aksnes 2004). Indeed, in the Black Sea, a close negative correlation between forage fish stocks and water clarity has been observed (Aksnes 2007). Increased eutrophication may also lead to increased occurrences of hypoxic conditions, something that also benefits jellyfish, because they are more tolerant of low oxygen levels than most other animals (Purcell 2012).

The reproduction of locally adapted jellyfish have in many instances been shown to increase with temperature (Purcell et al. 2012; Purcell 2012). With **climate change**, many seas are currently warming, and jellyfish are predicted to respond in a positive way (Purcell 2012).

Marine infrastructure also directly affects the ability of jellyfish to form large populations, the increase in artificial hard structures such as coast protection, habours, bridges, offshore drilling platforms, windmills and aquaculture pens have increased the availability of suitable substrate for cnidarian polyps, and the rise of fast and intensive shipping have increased the transportation of organisms through ballast water, leading to species introductions in many places. Because of their high growth rates, wide environmental tolerances and unselective feeding, jellyfish are ‘ideal’ candidates for invasive species, most succinctly exemplified by the originally American ctenophore *Mnemiopsis leidyi* which is now common in most European waters (Purcell et al. 2010; Schaber et al. 2011; David et al. 2015).

1.1.5 The state of jellyfish research

Historically, jellyfish have often been ignored by ecologists, as they were considered to be unimportant members of marine food webs, and consequently, they were not recorded in scientific survey trawls, or were actively excluded from capture (Brotz et al. 2012). This probably reinforced the perception of their unimportance, together with the variable and unpredictable nature of jellyfish populations. As a result, there is a lack of long or high quality data series of jellyfish populations, making it difficult to assess modern population sizes and distributions in a historical light (Brotz et al. 2012). Even today, though the ecological importance of jellyfish has been increasingly recognized in the last 30-40 years, jellyfish are still hard to sample, due to their large but fragile bodies and patchy distributions (Purcell 2008). Perhaps due to the lack of quality data, jellyfish was, at least until recently, still largely absent from ecosystem models (Pauly et al. 2009; but see Robinson et al. 2014). However, we do have a fairly good understanding of many aspects of the individual rates and processes of jellyfish, including vital rates and feeding traits (Acuña et al. 2011; Pitt et al. 2013; Kiørboe & Hirst 2014).

Perhaps spurred by the lack of field data, there are several examples of simpler, more theoretical models exploring aspects of jellyfish ecology, including clearance rates (Acuña et al. 2011), advective transport (Barz et al. 2006; Berline et al. 2013), local population dynamics (Ruiz et al. 2012) and competition with fish (Eiane et al. 1997; Oguz et al. 2008; Haraldsson et al. 2012), and mathematical models remain a promising tool for exploring the implications of hypotheses obtained from laboratory or other empirical studies, and for the development of new hypotheses regarding the dynamics and environmental control of jellyfish populations. There are still a lot we do not now about the ecological roles of jellyfish, including the relative importance of various environmental and ecological controls on global jellyfish populations, their effects on food webs and especially fish stocks, and how to develop predictive models capable of forecasting jellyfish populations.

Quality data on jellyfish distributions and population development might be scarce, but even less is known about the benthic polyps which form the source of most jellyfish blooms (Boero et al. 1996; Boero et al. 2008; Brotz et al. 2012). Because polyps are cryptic, being small and benthic, they are hard to observe, and since the polyps of different species look alike and do not resemble the adult medusa, identifying which polyp belongs to which species can be a daunting task. Recently, however, research on polyp biology has benefitted from new developments, primarily the cultivation of jellyfish polyps under laboratory conditions (but see Willcox et al. 2008), and our knowledge of the reproductive strategies, growth rates and environmental tolerances of jellyfish polyps have expanded considerably (Vagelli 2007; Prieto et al. 2010; Purcell et al. 2012; Melica et al. 2014; Schiariti et al. 2014; Schiariti et al. 2015). However, little is still known about

polyp population dynamics. For example, the question of what mechanisms govern the evolution and use of their various asexual reproductive modes, how polyp and adult medusa populations interact, and what the exact role of polyps in the formation of jellyfish blooms is, are still largely unanswered.

1.2 Modelling approaches

1.2.1 On the nature of models

All organisms sense their environment, chemically, by sight, hearing or otherwise, and the various senses that are available to organisms allow them to get information about the physical world around them. As human beings, through passive observation, the transfer of ideas between individuals and our own interactions with the physical world, we use the information gathered by our senses to form our perception and understanding of the world. In this way, every human being spends their life building their own vast mental version of the world, a version which is fundamentally unique to every person. However, though this understanding is always inherently an imperfect representation (a 'model' of the real world), it can be more or less accurate, and the defining ability that sets humans apart from the rest of the tree of life is the degree to which we are able to learn and build on the experiences of others.

At its core, science is a standardized method or process for the acquisition, standardization, evaluation and synthesis of experiences, and for sharing and coordinating it among individuals, all in order to form a shared, and internally consistent, theory or model of the make-up and functioning of the world. The fundamental elements of this process are the asking of questions about the world, the formation of hypotheses and subsequent derivation of predictions, and the testing of those predictions on the basis of comparisons with observations, leading to either formation or alteration of theory, or further hypotheses (figure 4).

Thus, the scientific method is an iterative and collective process, in which a common theory or model of the world (or a part of it) is formed and expanded, and all scientific descriptions of real world phenomena are strictly speaking models of reality, albeit with different levels of uncertainty. A model is a concept or idea of how a specific process or system functions. As such, drawings, diagrams, fitted lines or even descriptions are all examples of models. However, at least in the science of ecology, the term 'model' is in my experience most often taken as referring to a *mathematical* model, i.e., a mathematical description of some ecological process based on our understanding (or part of it) of that process.

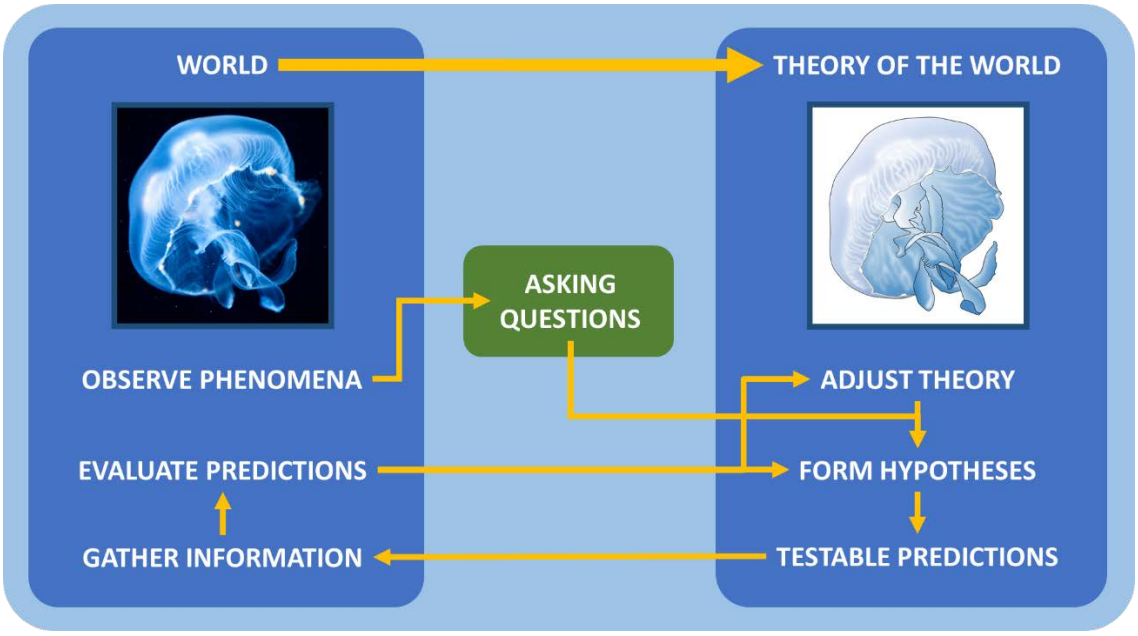

Figure 4. The basic elements of the scientific process. Based on observation of the real world (left), a theory of the world (right) is formed. The process starts when a new or unexpected phenomenon leads to the asking of questions about the world. These questions lead to the development of hypotheses about the nature of things, from which testable predictions can be derived. The predictions are then compared with real world observation, and the resulting rejection or acceptance of the hypotheses can either lead to the formation or alteration of theory, or to further hypotheses.

The use of mathematical descriptions of theory is a useful tool for many reasons. Math is based on logic, and describing processes in concrete terms using math makes the description precise and unambiguous, even for people with different backgrounds, cultures or languages. This concreteness makes mathematical models easier to analyze, and facilitates the understanding of abstract or complex phenomena that are not easily grasped or comprehended. The process of formulating mathematical descriptions can also help in revealing weaknesses and gaps in our knowledge. Math is the shared language of science and describing processes in mathematical terms, allows similar patterns and functional parallels to be identified across otherwise dissimilar fields, which allows the fruitful cross-pollination of ideas between, for example, economics and ecology. Moreover, and no less importantly, math lends itself to measurements and quantification, which gives objectivity and comparability to observations. When theory is also expressed as mathematical models, predictions can be quantifiable, and thus directly comparable to observations from the real world.

This thesis about jellyfish consists of three quite different examples of the use of mathematical models in ecology. In the following, I will discuss some of the motivations and considerations behind mathematical model studies in general and this thesis in particular, and in this context, I will use the terms model and mathematical model more or less interchangeably.

1.2.2 Fundamental approaches to mathematical models in ecology

Mathematical models are used for a variety of different purposes in ecology. Just as we may use different tools like experiments, field measurements and remote sensing to make observations, models can be useful for a range of processes on the theoretical side of science (figure 4, right side). At their core, models are idealized representations of the real world that are thought to retain some essential properties of the studied system (or a part of it). Models can be manipulated to form 'thought experiments', which can be useful for formulating new research questions at one end of the spectrum, and for running forecasting scenarios as a basis for management at the other. It is seldom feasible, affordable or ethical to conduct experiments on (or even monitor) whole ecosystems in ecology. Large models that are thought to more or less accurately reproduce the behavior of the ecosystem are therefore often used as a basis for management. These models are pieced together from many smaller observations and experiments, because they must include many different ecological processes in order capture the behavior of the whole system. No less important or useful, models with a narrower scope are used as a tool for the examining, developing and testing of hypotheses about some ecological process or component of interest. Using models, the ability of a new hypothesis to explain some a priori observed pattern can be explored, or predictions that follow from an established theory or hypothesis can be generated and then compared to observations.

When discussing the use of models in ecology, it is also important to distinguish between two fundamental approaches to models, i.e. phenomenological models and mechanistic models. A phenomenological model is based on patterns or relationships in data from field or experimental observations, and do not explicitly provide causal explanations for their dynamics or distributions. An example is the logistic model of density-dependent population growth, which is based on the fitting of the logistic equation to data on growing populations (Geritz & Kisdi 2012). In this model of population growth, the two parameters r and K (population growth rate and carrying capacity, respectively) regulate the growth and ultimate size of the population; however, it is not easy to explain how they relate to directly observable processes in nature, and it can easily be understood that independence between r and K is often not realistic. This is because, in nature, populations develop as a consequence of processes that occur at the individual level (i.e. birth and death), and while the logistic equation can often accurately predict the population size at a later time, it does not explicitly describe the processes that causes these dynamics.

In contrast, mechanistic models are ideally based on 'first principles', that is, established and fundamental processes that underpin the behavior of a system. To repeat our example of the logistic model, it can be derived from more mechanistic models that

are based on individual rates, (e.g. birth and death), and where the density-dependent relation comes from, e.g., interference between individuals which increases as population density increases (Geritz & Kisdi 2012). In this way, it can be shown that r and K are indeed related parameters, and that different relationships between them can be obtained with different mechanistic descriptions of the individual processes, thus adding a deeper layer of understanding to our model. Hence, mechanistic models allow for the direct examination of mechanisms and assumptions that lead to model results. Moreover, and in contrast with statistical approaches, mechanistic modelling relies on our level of understanding of the processes, while less so on the quality of the data collected for the system. This approach may therefore offer more robust predictions outside of the known conditions of the system, as for example when the climate changes to a state outside of our historical experience.

In reality, phenomenological and mechanistic modeling are not as clear-cut as they might seem. To quote Geritz and Kisdi (2012), *"Ecology will never be understood from quantum mechanics"*, and thus, even mechanistic models rely on predefined functions and distributions on some level. The question is where to draw the line of the level of detail, in the trade-off between a correct and detailed representation of key processes, and reducing the complexity of the model. Often, the key is to focus on mechanistic descriptions of the focal processes in a model, while reducing the level of detail on more well-established, or unimportant processes. As a rule of thumb, large scale management models of complex systems, like models of entire ecosystems (see figure 5), are often based largely on patterns drawn from large amounts of data, while simplified models aimed at examining and understanding some specific process are often more mechanistic. In an ideal world, larger scale phenomenological models are generalized from many smaller scale mechanistic models that provide the mechanistic underpinning and justification of the larger model.

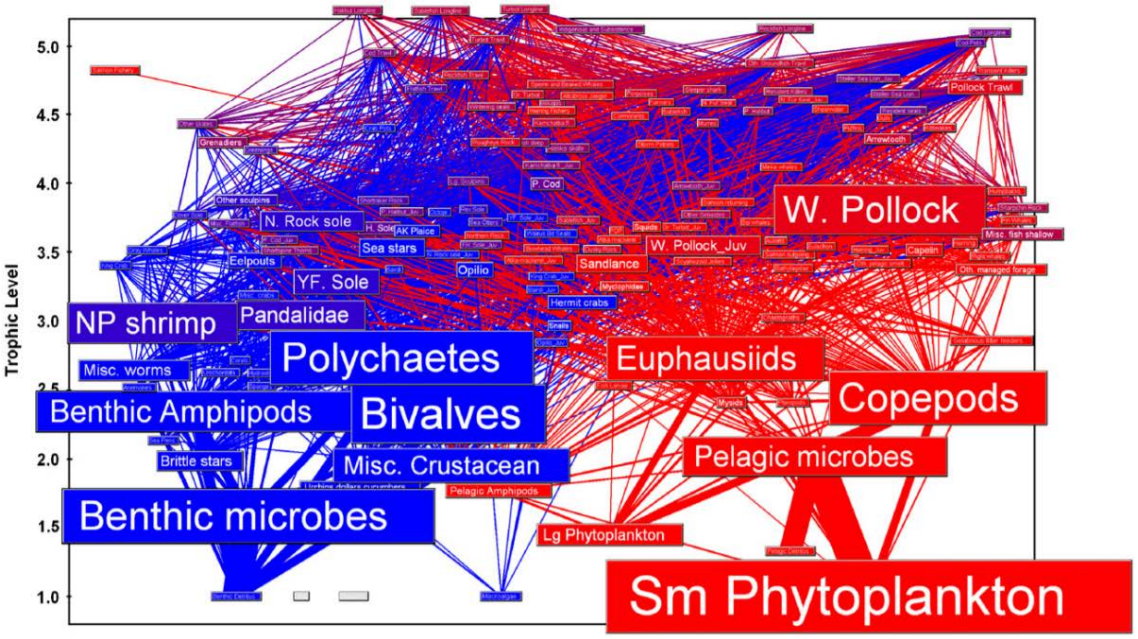

Figure 5. An example of a complex contemporary food web model of the Eastern Bering Sea food web. This mostly phenomenological model is based on biomasses and diet compositions (assuming mass balance) estimated from observational data. Reprinted from Aydin and Mueter (2007).

1.2.3 Some important considerations for model studies

In theory, if a model as complicated as the real world could be devised, it would be able to simulate its behavior perfectly (at least if not for quantum mechanics and the Heisenberg principle). Long before such a level of complexity was reached, however, the model would be as difficult to understand and interpret as the real world, and thus, more or less useless. In reality, a good model is a compromise between many considerations that trade off against each other, of which the most important pairs are that of model specificity against generality, and that of tractability, analytical ease and computational requirements against level of detail and complexity.

By keeping a model general, that is, ensuring that its descriptions and processes are common across many different systems and situations, it can retain a broad applicability, which is useful when dealing with broad patterns in ecology; on the other hand, if more detailed and specific descriptions are used, the model is more likely to be a more accurate description of the system it is specific to, but will then be specific to those cases. On the technical side, the more detailed and complex a model is, the harder it is to manage, rapidly becoming difficult to analyze and understand, and more likely to require too much computational time.

Another downside of model complexity is the growing number of parameters that the model will depend on as it gets more detailed. All parameters come with some uncertainty, and as more and more uncertain parameters are added, this uncertainty can often accumulate to levels that make the model results weaker at best, and useless at

worst. Uncertainty and sensitivity analyses can often contribute valuable insight on key parameters and processes, and this information is well used in an effort to reduce the number of superfluous parameters, and identify ones that require more attention.

Most of these considerations above can be considered as questions of scale, i.e. the resolution of the model along different dimensions of space, time, ecological coverage and resolution and environmental variability. When dealing with a model of higher trophic levels, for example, it is most often not necessary to model primary producers in detail. Likewise, a model of phytoplankton competition might not need spatial dynamics, and a model of long-term population dynamics might not need to consider short-term environmental fluctuations. Determining all the correct level of scale on all these dimensions is the primary task of a modeler, and the easiest way to go about it is often to consider the specific research question that is the motivation of the model study, and asking what the minimum number of components that are needed to adequately answer the question. As such, the most important methodological bench-mark for a model is that it adequately reproduces the characteristic and essential features that are needed in the context of the subject of interest or the problem to be solved, without being unnecessarily complicated.

Last but not least, an important consideration for the design of any scientific model is the question of the evaluation and validation of the results. Models should produce output of a nature that is directly comparable to observations. Verifying that a model behaves in a manner that is consistent with nature does not necessarily prove that the model is correct - but the reverse is certainly true, and shoving that the model can reproduce patterns from nature is a crucial step in any model study. This is especially important for predictive models that are supposed to be used as a basis for management decisions. Such management models need to be rigorously tested against good quality data, in order to give credibility to any forecasting. In this context, to quote Ray Hilborn (2016): *"A model without data is like sex without a partner - a pastime for adolescents, but not the full experience"*. Even for models whose primary purpose is to develop hypotheses and examine theory, being able to compare patterns and outcomes with nature is valuable, especially if the purpose of the model is to generate testable predictions. While it is often not necessary to generate accurate numerical predictions, even qualitative results need to be stated in precise terms that can be directly tested against empirical evidence.

1.2.4 The trait-based approach to ecological models

All organisms consist of cells, either solitary or, in the case of multicellular organisms, in aggregate. Moreover, all organisms ultimately originate from the same cell, have genomes that are made of DNA and must fulfill the three basic missions of life in order to thrive and persist, that is, they must require resources, survive, and reproduce. To this end, all living things must balance their morphology, physiology and behavior to best accommodate the three missions, which are often in conflict with each other. Despite these common origins and requirements, organisms have evolved in many directions, and the most striking property of life on earth is its immense diversity, as well as the complexity of the interactions between organisms. As discussed in previous sections, this complexity also inherently hinders our efforts to describe and predict how ecosystems function and evolve. The challenge is to describe and explain ecosystems in a sufficiently accurate way, without making the description as complex as the real world.

One approach to marine ecosystem research which has gained increased attention in recent years is the so-called 'trait-based approach' (Bruggeman & Kooijman 2007; Litchman et al. 2013; Andersen et al. 2015). In the trait-based approach, organisms are considered in light of the unique set of traits (e.g. size, the "master trait", see Andersen et al. 2015) that define how they function and interact with the rest of the ecosystem. A trait, in this context, is any characteristic of an organism that contributes to determine its fitness (Litchman et al. 2013). As species, and ultimately ecosystems, evolve through this trait-space, they move along the lines of trade-offs (between the costs and benefits of a trait) which can be inherent to a certain trait, or occur between traits due to restrictions on resource or time allocation or to more fundamental conflicts between two traits. The trade-offs associated with a certain trait depend on the environment surrounding the organism, and as the environment or other organisms evolve and change, trade-offs also change, and the traits of an organism must also evolve in response. Thus, ecosystems evolve through the complex interplay between individuals, the environment and other organisms. In a trait-based framework, individuals can be considered as points in a multidimensional space, with all the possible traits forming the axes. Hence, instead of viewing an ecosystem as a (static) collection of discrete and unique species or functional groups, it can be described as the volume in this continuous trait space that is able to represent all the organisms that are in it.

In more practical terms, there are two main ways in which the trait-based approach can be applied to ecological modeling. First, the increasing number of functional groups added to traditional ecosystem models (figure 5) can be reduced by representing the key guilds (e.g. phytoplankton, zooplankton) as single entities characterized by key traits. These traits can evolve in response to environmental pressures, along the lines of their trade-offs (see Bruggeman & Kooijman 2007 for an example). Second, smaller theoretical

models are used, not to model an entire ecosystem, but to examine the trait-offs and ecological consequences of isolated traits (e.g. Mariani et al. 2013). This second application of the trait-based approach is in use in all three of the model studies within this thesis.

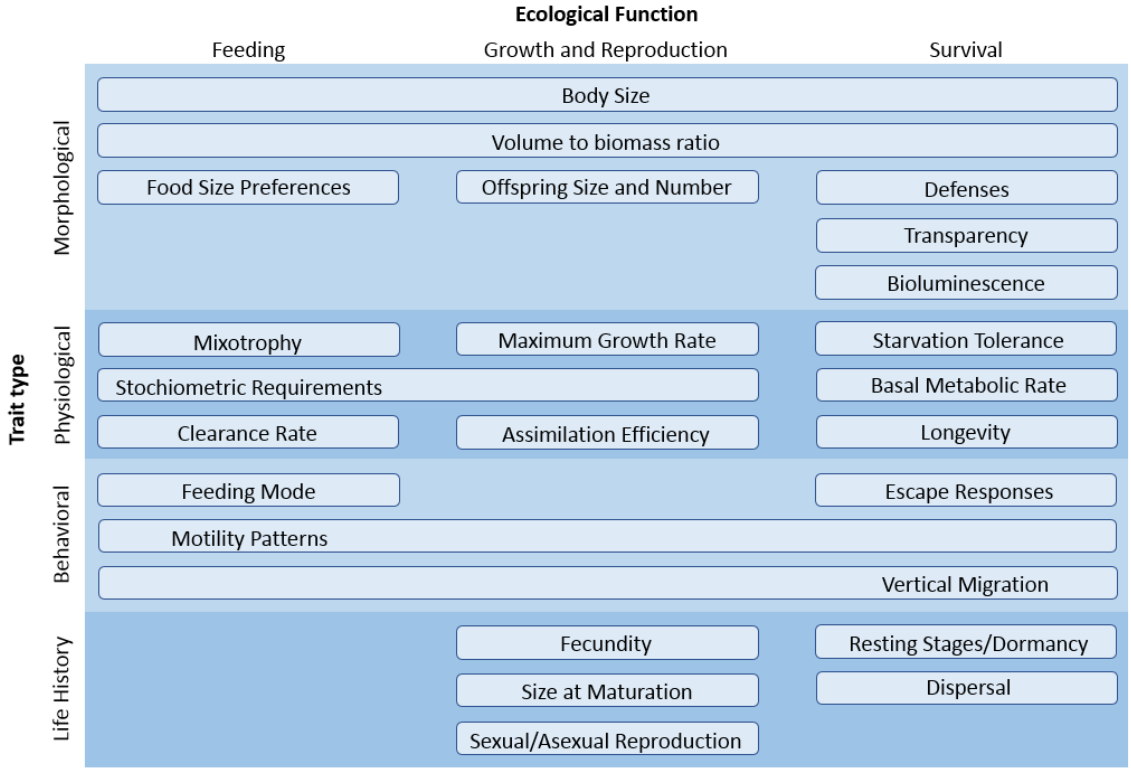

***Figure 6. Examples of typical zooplankton traits, classified according to function and type. Some traits (like body size), has important implications for all three functions, and all traits influence the others to a variable degree. Figure based on Litchman et al.* (2013).**

Chapter 2. **Three models**

This chapter contains brief summaries of the three studies that form the basis of this thesis. The three studies are quite different, and each focus on an important aspect of jellyfish ecology, with emphasis on how the unique traits of jellyfish interact with the environment to regulate jellyfish population dynamics.

As discussed in section 1.1, jellyfish share many common traits that set them apart from other organisms, such as their inflated and simple body plans, fast growth rates and reproduction, efficient swimming and feeding, and high clearance rates. In the first study of this thesis, we examine the competition between forage fish and large zooplanktivorous jellyfish, as influenced by water clarity through their contrasting feeding traits. Because of the fundamental nature of the competition for the common food resource and this feeding trait difference, we investigated the ability of water clarity to generate observed global occurrences of jellyfish blooms.

In spite of their similarities, different jellyfish can have fundamental differences in key traits, such as feeding mode and life cycle. In the second study we investigated how environmental variation can contribute to the fluctuating nature of jellyfish populations. We mainly focused on how the two fundamental life cycles of jellyfish could be expected to respond to different environmental variations. The third study was dedicated to the important, but understudied polyps of scyphozoan jellyfish (see section 1.1.3), and their plastic and complex asexual reproductive biology. Using an evolutionary model, we investigated the evolution of multi-mode reproductive strategies and their interactions with environmental conditions.

Related to their different subjects, the three studies also represent different approaches and scales of models. All three focus on the functioning and environmental or evolutionary implications of key jellyfish traits, however, whereas the first two studies are food web models concerned with adult jellyfish populations and their interactions with the rest of the ecosystem, the third study focuses on the evolutionary aspects of jellyfish polyps. Moreover, while the first study considers a relatively simple and general model that can be analytically solved and applied in a global context, the second considers a more limited situation, but is richer in details and complexity. As such, the three models provide examples of how theoretical mathematical models like these are a flexible tool than can be tailored to specific situations and questions.

Jellyfish are underrepresented in ecosystem models, but understanding the role and regulation of jellyfish populations has proven to be an important aspect of the management of marine system (Pauly et al. 2009). There is therefore a drive to better

understand and describe jellyfish population dynamics. However, compared to the study of fish or crustacean zooplankton, jellyfish have received much less attention in the past, and our knowledge base is therefore much more limited, especially when it comes to the availability of long and comprehensive data series (Brotz et al. 2012). This however, provides an opportunity to form our understanding of the roles of jellyfish in marine systems from the 'bottom up', constructing mechanistic descriptions of the key traits and features that sets jellyfish apart, and then comparing the predicted dynamics to the data and observations that are available. Such models can help piece together the key interactions for developing predictive capabilities when it comes to jellyfish populations; however the three studies herein also highlight the need for more field studies, in order to validate the predictions of models.

In the following, I will briefly present the background, motivation, approach and main conclusions of the three studies.

2.1 Modelling the competition between fish and jellyfish

Competition for shared zooplankton resources between fish and jellyfish have been suggested as a contributing cause of both jellyfish proliferations and fisheries collapses. Numerous examples of reverse trends of fish and jellyfish populations are given in the literature, e.g. in the Black Sea (Daskalov et al. 2007), in Scandinavian fiord systems (Eiane et al. 1999; Riisgård, Andersen, et al. 2012), as well as in larger coastal areas (Roux et al. 2013), to name a few. It is, however, difficult to obtain direct evidence of competition, and can be even harder to disentangle the causal chain of events which gives rise to such patterns (e.g. Llope et al. 2011).

In addition, competition between fish and jellyfish is not expected to play out equally in all environments, due to key trait differences between fish and jellyfish, most importantly in their modes of feeding. While fish are efficient visual predators that detect their prey from a distance, jellyfish are tactile predators that do not rely on sight. This means that fish and jellyfish are expected to respond differently to deterioration of water clarity, which can arise through e.g. anthropogenic eutrophication. Another anthropogenic pressure which affects fish and jellyfish unequally is fishing, which mainly targets fish species, and so it seems likely that increased fishing pressure on forage fish will affect their competition with jellyfish in favor of jellyfish. While the local intensity of fishing or eutrophication may vary across the globe, their effect on the competition between forage fish and jellyfish are universally applicable across species and environments. Thus, these are examples of environmental factors with potentially global relevance for jellyfish populations worldwide.

In the first study of this thesis, we explored the hypothesis that productivity, water clarity and fishing, can regulate the outcomes of competitive interactions between fish and jellyfish. We further hypothesized that differences in these environmental conditions between separate areas could explain the global patterns of jellyfish occurrences.

To this end, we assembled a food web model containing zooplankton, jellyfish forage fish and predator fish, representing the typical relative positions of fish and jellyfish in marine food webs. This aspect of the model was kept intentionally simple, for the joint purposes of ensuring the general applicability of the model, as well as its analytical tractability. We used detailed mechanistic descriptions of the feeding modes of fish and jellyfish, especially the dependence of forage fish feeding on visual characteristics of the water. The model was parameterized assuming fixed typical sizes of individuals within of the modelled groups, and using published allometric relationships for their vital rates. To simulate parameter variation due in part to uncertainty, but especially variation in species composition across locations, we used the Monte Carlo method to determine model outcomes across a wide range of different parameter combinations, and developed an index describing the distribution of model outcomes between fish and jellyfish exclusion.

We then applied the model to global data sets of light, water clarity and primary production from satellite observations to produce maps of the likelihood of different model outcomes in coastal areas. The model predicted regions of coexistence and competitive exclusion of either jellyfish or fish, depending on a combination of water clarity, productivity and fishing pressure. We also predicted an interaction between fishing pressure and water clarity, where increased levels of either reduce the threshold of the other at which fish are excluded from the system.

Although there is a both qualitative and quantitative lack of good data on the global distributions of jellyfish to compare with, the model reproduced the known distributions of coastal jellyfish occurrences relatively well. We concluded that the effect of reduced water clarity acting through key trait differences between fish and jellyfish could, to a large extend, explain observed patterns of jellyfish occurrences, and that the sudden regime shifts to a jellyfish-dominated state observed in some systems, could in part be explained by a combination of the fast-acting pressure of fisheries and the slow-acting pressure of eutrophication.

2.2 Seasonal jellyfish blooms and the importance of life cycle

Jellyfish blooms are mainly a coastal phenomenon and the highest biomasses are consistently found in enclosed or semi-enclosed areas, where advective losses are low (see e.g. Olesen et al. 1994; Lucas & Williams 1994; Beaulieu et al. 2013). The timing and magnitude of jellyfish blooms are often extremely variable and unpredictable, but usually have a seasonal component in temperate areas (Riisgård, Madsen, et al. 2012; Condon et al. 2013). However, while sometimes seemingly stochastic in nature, jellyfish blooms must, if not follow, then at least require as a prerequisite, sufficiently favorable environmental conditions in order to form blooms.

Apart from suitable conditions, the propensity of jellyfish to bloom depends on their traits, and jellyfish generally share many traits that allow them to rapidly capitalize on favorable conditions (see section 1.1). One key trait which varies fundamentally within jellyfish is the life cycle. As mentioned in section 1.1.3, jellyfish life cycles generally separate into two main types: metagenic jellyfish and holoplanctonic jellyfish, but it is unclear what the trade-offs involved are, and if and how these two types differ in their response to environmental variation.

In the second study, we wanted to examine the hypothesis that the different functioning of the two life cycles entail differences in their response to environmental seasonality and variation. The second aim of the study was to examine the ability of environmental variation and seasonality to explain the erratic nature of jellyfish blooms. More specifically, we explored advective losses of jellyfish as our chosen variable, its ability to regulate local jellyfish populations, and whether and how the two main types of life cycle would be expected to respond differently to this variation.

We used a chemostat formulation of an idealized seasonal coastal ecosystem, where the turnover of nitrogen, phytoplankton, zooplankton and two types of jellyfish (holoplanktonic and metagenic) is regulated by the water exchange rate, simulating a semi-enclosed system where water is exchanged with a larger external source, and assuming no jellyfish in the outside system. Holoplanktonic jellyfish was modeled as a simple biomass box, assuming constant reproduction and average size, which is a fair approximation for a generally small holoplanktonic jellyfish with larval reproduction (see section 1.1.3). To capture the typically pulsed and cohort-like nature of temperate metagenic jellyfish populations, we separated their biomass into abundance and individual size, accounting for the simultaneous seasonal decrease in numbers and increase in size typical of such jellyfish. A new cohort of small individuals was added every spring, simulating the release of ephyrae (see section 1.1.3), and the (few) survivors

were removed in the fall. To focus on the effect of life cycle, the two jellyfish types were assumed to be identical in all other aspects.

Environmental variation on water exchange was split into a seasonal component and an autocorrelated random component. Simulations were run with varying levels of seasonal signal strength and autocorrelation on the random signal, and the resulting time series of jellyfish, zooplankton and phytoplankton compared.

The chemostat model reproduced the typical seasonal dynamics of the main plankton groups in temperate coastal ecosystems and models thereof. Moreover, the model predicts a top-down trophic cascade in years of high jellyfish biomass, leading to suppressed zooplankton biomass and a summer bloom of phytoplankton. Such a jellyfish-induced trophic cascade is also consistent with observations from natural ecosystems (Huntley & Hobson 1978; Schneider & Behrends 1998; Møller & Riisgård 2007b). Interannual variation in the water exchange rate produced fluctuations in jellyfish biomass reminiscent of wild populations, but the level of autocorrelation in the water exchange time series were important for the extent to which the variation in water exchange rate translated into variation in jellyfish population sizes. We also found that the dependency of holoplanktonic jellyfish on winter survival translated into a typical late-season bloom, compared to that of metagenic jellyfish, a pattern that was reinforced by the increasing late-season allocation of resources into reproduction by the metagenic jellyfish. Generally, holoplanktonic jellyfish biomass seemed more variable than that of metagenic jellyfish, and was also more interannually autocorrelated. An interesting prediction of the model was that seasonality was predicted to favor metagenic jellyfish. Unsurprisingly, apart from the rate of advective loss, the metagenic jellyfish were mainly dependent on the magnitude of the spring release of ephyrae.

Lacking data sets combining observations on water exchange rate and jellyfish populations, we showed that our dynamics and predictions are consistent with numerous cases from the literature, most frequently on *Aurelia* sp. or *Mnemiopsis leidyi*. Our results suggest that environmental fluctuations as a trigger for jellyfish blooms should be explored more, as opposed to only considering average environmental conditions, and underlines the potential importance of life cycles for jellyfish population dynamics.

2.3 The evolution of asexual reproduction in jellyfish polyps

Most observations of coastal jellyfish occurrences are of scyphozoan cnidarian jellyfish (see section 1.1), who in most cases have a metagenic life cycle characterized by small, inconspicuous benthic polyps. Many aspects of polyp ecology are still poorly illuminated, however, the importance of these polyps for the population dynamics and bloom potential of metagenic jellyfish is increasingly recognized (Lucas et al. 2012).

One fascinating aspect of polyp ecology which also has important implications for adult jellyfish blooms is the various modes of asexual reproduction employed by scyphozoan jellyfish polyps (Schiariti et al. 2014). While all jellyfish polyps can produce adult medusae through strobilation, most can also produce additional polyps through several modes of clonal reproduction. These polyp-to-polyp reproductive modes can generally be sorted into three separate categories based on their function: 1) locally retained buds; these grow from the parent polyps, and can usually start feeding before reaching full size and detaching, resulting in fast reproduction. 2) resting cysts that are resistant to predation, starvation and other sources of mortality, but require a specific environmental signal to hatch into a new polyp, resulting in a slower potential growth rate. This mode is very common across scyphozoa. 3) production and release of motile buds. These can be very small or larger, but all types go through a mobile phase and do not attach and start to develop until after a period of time of several days to weeks. As the number of polyps at the time of strobilation essentially determines the number of adult jellyfish in a cohort (see the previous section), the effect of these three modes on polyp growth and response to environmental conditions has important implications for adult jellyfish populations.

We therefore wanted to investigate the trade-offs associated with these three modes of asexual reproduction, and what conditions might favor their evolution and coexistence in jellyfish polyps. We drew inspiration from the literature on the evolution of asexual reproduction, dispersal and dormancy strategies in plants, and built a model of the competition between two polyps with different allocations of reproductive resources to the three modes. As the reproductive mode of motile buds has a spatial component (dispersal), the model needed to have a spatial dimension, and we therefore designed the model as a metapopulation-type model, exploring the effect of different values of local extinction risk and the relative return of investment (fitness) of the three strategies.

Using an evolutionary algorithm where the allocation to the three reproductive modes was allowed to evolve through mutation and selection, we were able to estimate the

Evolutionary Stable Strategy for a given parameter set, that is, a strategy which outcompetes all other strategies. For all parameter values explored we found that a single ESS was present, and this ESS was always characterized by more than one mode of reproduction, except in the extreme cases where the local extinction risk was zero or one. Generally, as the extinction risk increased from zero, the ESS changed from being dominated by fast local budding towards increasing allocation to cysts and/or motile buds, depending on their relative fitness. At intermediate extinction risk, and when the relative fitness of cysts and motile buds was unequal, the ESS was usually a two-mode strategy, however, when the extinction risk increased to high levels, a strategy with allocation to all three strategies was selected.

The prevalence of multi-mode strategies was found to be consistent with observations, as were the prediction that local budding should dominate the strategy under ideal conditions, and the prediction that cyst production should be a response to increasing mortality. In nature, cyst production seems to be the most ubiquitous mode, and we found that if extinctions are spatially correlated, as would be expected for many naturally occurring causes of extinction, the production of cysts is favored, possibly providing an explanation for the dominance of this mode among scyphozoan jellyfish polyps.

However, we also predict that motile buds should be favored in 'risky' and patchily fluctuating environments, where their rapid recolonization of empty patches causes them to be selected. This prediction, along with our general prediction that the presence of multi-mode strategies should be favored by high extinction risk for polyps are new hypotheses which can be tested against observations. Our study is a fist systematic attempt to consider polyp asexual propagation as a whole, providing a framework to understand the functioning, environmental interactions and trade-offs involved.

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Chapter 3. **Manuscript I**

The global susceptibility of coastal forage fish to competition by large jellyfish.

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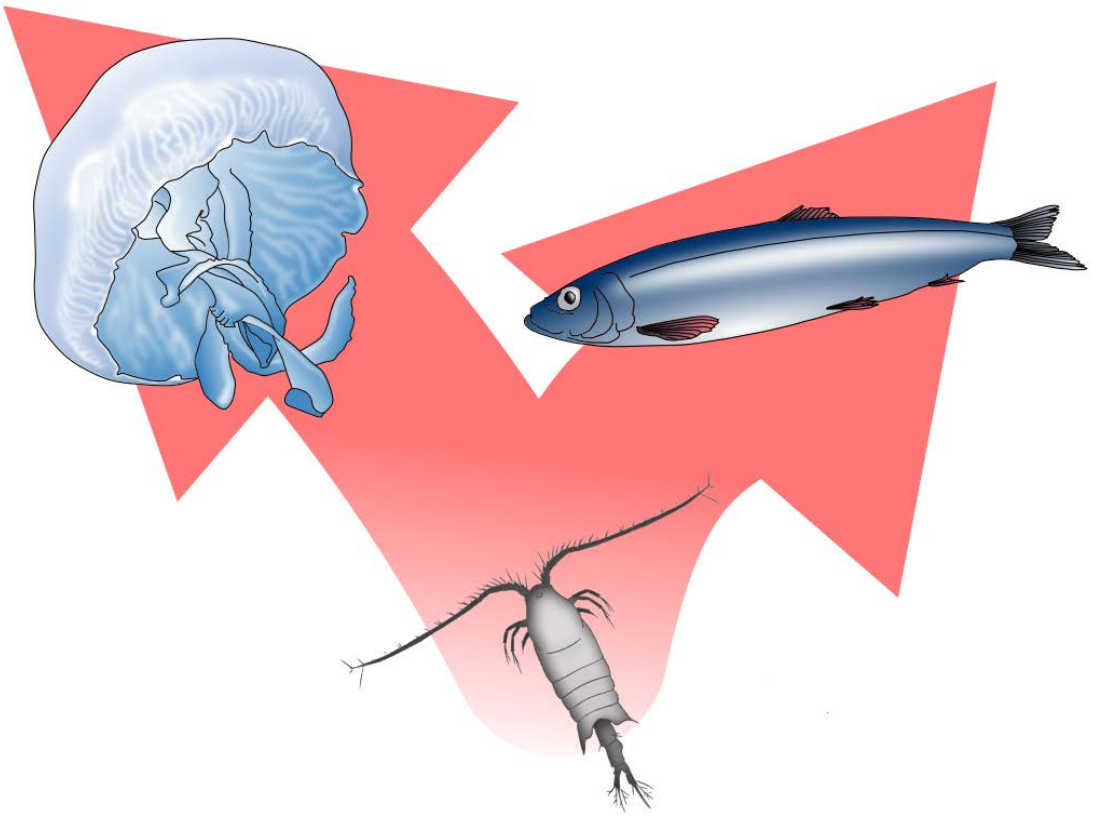

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THE ROYAL SOCIETY PUBLISHING

The global susceptibility of coastal forage fish to competition by large jellyfish

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Competition between large jellyfish and forage fish for zooplankton prey is both a possible cause of jellyfish increases and a concern for the management of marine ecosystems and fisheries. Identifying principal factors affecting this competition is therefore important for marine management, but the lack of both good quality data and a robust theoretical framework have prevented general global analyses. Here, we present a general mechanistic food web model that considers fundamental differences in feeding modes and predation pressure between fish and jellyfish. The model predicts forage fish dominance at low primary production, and a shift towards jellyfish with increasing productivity, turbidity and fishing. We present an index of global ecosystem susceptibility to shifts in fish–jellyfish dominance that compares well with data on jellyfish distributions and trends. The results are a step towards better understanding the processes that govern jellyfish occurrences globally and highlight the advantage of considering feeding traits in ecosystem models.

1. Introduction

During the last few decades, the ecology of pelagic cnidarians and ctenophores has attracted increasing attention and has raised public concerns about their impact on our societies [1]. This was sparked by spectacular cases where jellyfish have proliferated, causing extensive economic damage [2,3] and dramatic changes of the local ecosystem structure [4–7] with alternate ecosystem states [7,8]. The species responsible for these changes are almost exclusively large, feeding-current feeding types [2,9], and we refer to these types as 'jellyfish' throughout this study.

Jellyfish are generally considered unwanted or harmful and can cause direct damage to tourism, infrastructure and fishing gear [2]. They also have more indirect impacts on ecosystem functioning, as certain jellyfish and forage fish (small pelagic zooplanktivorous fish) feed at a similar trophic level [4–6,8,10,11]. Additionally, many jellyfish can be locally important predators on the younger life stages of fish [3,12]. Competition is notoriously difficult to prove [12] but environmentally induced changes in the ability of jellyfish to compete with fish are likely a cause of jellyfish proliferation and can have large negative impacts on both ecology and economy. Forage fish are not only targets of important fisheries, but are also the main prey for high-value predatory fish, as well as for many seabirds and marine mammals [3]. Thus, a better understanding of the factors governing the competition between fish and jellyfish is important to predict patterns in jellyfish abundance and distribution. In particular, changes in competitive interactions may be responsible for the observed shift towards jellyfish dominance in certain ecosystems affected by climatic and anthropogenic pressures [3,13].

Despite recent advances in mapping global jellyfish distributions, blooms and temporal variation [1,14,15], most studies are on a local scale, and have revealed a host of environmental and anthropogenic factors promoting jellyfish (reviewed in [16]), including overfishing of fish [13], eutrophication [17],

reduced water clarity [18,19], changing oxygen availability [15], changes of benthic substrate [20] and introduction of alien species [21]. The large variety of both environmental conditions and species compositions across ecosystems makes it hard to identify general mechanisms that can be scaled up to the global level. To understand global patterns in jellyfish distribution and impact on forage fish in both time and space, we need to focus on fundamental properties transcending taxa and systems.

A fundamental difference between forage fish and jellyfish is in how they feed. While the visual feeding mode of fish is very efficient under good visual conditions, their clearance rate decreases with decreasing visibility, whereas the tactile feeding of jellyfishes does not [19,22,23]. Turbid conditions, owing to high phytoplankton biomass or terrestrial run-off, generate low light penetration in the water column and therefore tend to favour jellyfish over fish communities, as has been shown in Norwegian fiord systems [18]. A close correlation between optical conditions and forage fish biomass has also been found in the Black Sea [24], where extensive jellyfish blooms have coincided with crashes in forage fish populations.

In addition, whereas many predators are primarily dependent on forage fish for prey, jellyfish are typically consumed opportunistically by a broad range of predators [25,26], including fish [12]. Thus, forage fish may be subject to tighter trophic control than jellyfish and are often targets of important commercial fisheries [3]. Food web structure, exploitation and feeding ecology may thus cause jellyfish to be dominant in pelagic ecosystems heavily affected by eutrophication, high water turbidity and fishing, as it has been suggested by other modelling studies [23,27].

The overall ecological role of jellyfish in marine ecosystems is not yet well understood, but we do have a fairly good understanding of cnidarian and ctenophore autecology, including physiological traits such as elemental composition, allometric scaling of vital rates and locomotion [28–30], life-history (e.g. [31]) and feeding traits [28,32]. Here, we make use of this information to build a model of the fish–jellyfish competitive interaction by using mechanistic descriptions of processes at the individual level, to gain insights into the response of the system to changes in the environment. Basing the model on mechanisms that are common across all environments and taxa allows us to make it general enough to be applied in a global setting. The aim is to investigate to what extent feeding traits in fish and jellyfish populations can describe competition for food and explain some of the observed global patterns in jellyfish occurrence.

As the focus is on trophic interactions between large jellyfish species and fish populations, additional factors such as temperature effects on population growth and intraguild predation of fish and jellyfish during ontogeny are not explicitly addressed here, although the sensitivity of our results to temperature changes is considered.

2. Material and methods

(a) System formulation

Our food web model describes competitive interactions between a small pelagic forage fish (*F*, representing species such as anchovy, sprat or the like) and a cruising feeding-current feeding jellyfish (*J*, representing medusae such as *Aurelia aurita*, or ctenophores such as *Mnemiopsis leidyi*), competing for zooplankton prey

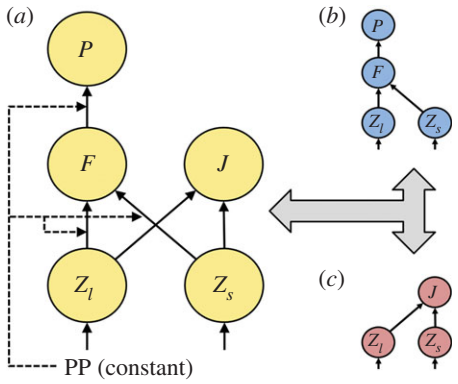

Figure 1. Idealized food webs describing (*a*) jellyfish and fish competition for zooplankton resources. The coexistence of all species in the food web depends on organism traits and environmental conditions, and changes in either of these may produce different food web configurations dominated by either (*b*) fish or (*c*) jellyfish. Primary production supports the food web and may also impact fish predation through changes in turbidity.

(figure 1*a*). The coexistence of jellyfish and fish in the food web is dependent on both environmental conditions (primary production, light) and individual parameters, and changes in either may define different food web configurations where fish and jellyfish do not coexist (figure 1*b*,*c*). We consider two size groups of mesozooplankton (Z_l and Z_s), to allow for differences in selectivity for prey size between fish and jellyfish. Our food web contains a predator fish (*P*, representing larger pelagic predators, fish such as tuna, cod, etc.) that predates upon forage fish, but not on jellyfish.

We let the food web be forced by primary production R (g C m^{-3} d^{-1}) that is converted into mesozooplankton biomass with transfer efficiency T_Z (dimensionless) [33]. We furthermore assume global assimilation efficiency f (dimensionless), and a production ratio between small and large zooplankton z (dimensionless). In the population model, we convert carbon mass to individuals using the body carbon mass w_i (g C ind^{-1}) of an individual of species i (electronic supplementary material, tables S1 and S2).

The food web is then represented by five coupled differential equations:

$$\frac{\partial Z_l}{\partial t} = \frac{RT_Z}{w_{Z_l}}(1-z) - (\beta_{F.Z_l}F + \beta_{J.Z_l}J)Z_l - m_{Z_l}Z_l, \tag{2.1a}$$

$$\frac{\partial Z_s}{\partial t} = \frac{RT_Z}{w_{Z_s}}z - (\beta_{F.Z_s}F + \beta_{J.Z_s}J)Z_s - m_{Z_s}Z_s, \tag{2.1b}$$

$$\frac{\partial F}{\partial t} = f\left(\frac{w_{Z_l}}{w_F}\beta_{F.Z_l}Z_l + \frac{w_{Z_s}}{w_F}\beta_{F.Z_s}Z_s\right)F - \beta_{P.F}FP - (m_F + y_F)F, \tag{2.1c}$$

$$\frac{\partial J}{\partial t} = f\left(\frac{w_{Z_l}}{w_J}\beta_{J.Z_l}Z_l + \frac{w_{Z_s}}{w_J}\beta_{J.Z_s}Z_s\right)J - (m_J + \partial_J)J \tag{2.1d}$$

and

$$\frac{\partial P}{\partial t} = f\frac{w_F}{w_P}\beta_{P.F}FP - (m_P + \partial_P)P. \tag{2.1e}$$

where $\beta_{i,j}$ is the clearance rate of predator i on prey j (m^3 ind^{-1} d^{-1}) and m_i, ∂_i and y_i are, respectively, the specific respiration rate, natural mortality and fishing mortality on species i (all in units of d^{-1}). Note that this model formulation does not include direct trophic interactions (i.e. predation) between the jellyfish and the fish.

Although jellyfish can effectively feed on fish early life stages [12], and sometimes may control forage fish recruitment [34], we think that such cases are strongly dependent on local jellyfish populations being very abundant at both the time and place of spawning. In addition, many forage fish have nursery or spawning sites that are separate from the pelagic, and the extent of jellyfish predation on forage fish larvae or eggs is largely species

specific. For these reasons, we think that at the scale we apply our model (large marine ecosystems) and for the generality of our results, those interactions are of secondary importance with respect to competition for food.

(b) Mechanistic description of feeding interactions

(i) Fish

We assume a fish swimming through the water with velocity v_i (m d^{-1}). The fish scans the surrounding water for prey within an average visual range $\bar{r}_{ij}$ (m), and a limited visual field defined by the visual half angle θ_i (°). On encounter, prey is captured with a probability A_{ij}, yielding the following clearance rate:

$$\beta_{ij.\mathrm{fish}} = A_{ij}\pi d(\bar{r}_{ij}\sin\theta_i)^2\sqrt{v_i^2+v_j^2}, \tag{2.2}$$

where v_j denotes the swimming velocity of the prey (m d^{-1}). The visual range depends on the light regime, the optical properties of the water, prey size, colour and shape, and on characteristics of the predator eyes. Here, we use a model of visual range by [22]

$$r_{ij.Z}^2 e^{cr_{ij.Z}} = |C_j|a_j E_i' \frac{Ie^{-K_d Z}}{K_e + Ie^{-K_d Z}}, \tag{2.3}$$

where $r_{ij,Z}$ is the visual range at depth Z, c is the beam attenuation coefficient (m^{-1}), C_j is the inherent prey contrast, a_j is the image area of the prey (m^2), E_i' is a compound visual processing parameter [35], I is the irradiance (µE photons m^{-2} s^{-1}) just below the surface, K_d is the light attenuation coefficient (m^{-1}) and K_e is the half-saturation constant for the visual system of the predator (µE photons m^{-2} s^{-1}). $r_{ij.Z}$ was estimated for each depth interval using a numerical solver, and then averaged over depth $Z_{\max}$ (m) to yield the depth-averaged visual range:

$$\bar{r}_{ij} = \sum_{Z=1}^{Z_{\max}} \frac{r_{ij.Z}}{Z_{\max}}. \tag{2.4}$$

(ii) Jellyfish

We consider a large feeding-current feeding jellyfish. Although the morphology of feeding structures and method of capture varies enormously, jellyfish of this type all swim continuously, displacing water in a cross-sectional area with a diameter equal to the maximum width of the animal and perpendicular to the swimming direction [28]. A certain proportion of this water passes through the capture apparatus, where prey is filtered out of the water with a certain efficiency. Thus, the clearance rate will be proportional to the velocities of prey and predator (v_i and v_j), the cross-sectional area of the animal and the filtering efficiency S [28]:

$$\beta_{ij.\mathrm{jelly}} = S\pi\left(\frac{L_i}{2}\right)^2\sqrt{v_i^2+v_j^2}, \tag{2.5}$$

where L_i (m) is the maximum diameter of the jellyfish in the plane perpendicular to the swimming direction. The filtering efficiency S combines the probability of capture with the fraction of displaced water coming into contact with the capture surfaces.

(c) Parameter estimation and model evaluation

Many of the parameters considered in our model are size dependent. However, including ontogenetic development would require a more complex, physiologically structured model. Instead, we parametrize the model using a specific reference size for each model population. Species-specific parameters are calculated from carbon content using group-specific allometric relationships (electronic supplementary material, table S2), and a comparison of the resulting clearance rates with observations verifies that the model yields realistic rates (see the electronic supplementary material, figures S3 and S4). When solved numerically, the model (equation (2.1)) converges towards a steady state. Six non-trivial and biologically meaningful equilibria can be derived analytically, all but one (figure 1*a*) being food web configurations with one or more missing species.

The global patterns of competition between forage fish and jellyfish in terms of productivity and optical conditions are explored by applying the model to the Large Marine Ecosystems (LMEs, see §2d), at a 0.5°-grid resolution. We exclude Arctic and Antarctic regions, because of a lack of reliable data on primary production and turbidity in those regions. We limit our analysis to the LMEs because jellyfish bloom occurrences are better documented there, allowing comparisons between predictions and observations.

A Monte Carlo scheme is used in each grid point to evaluate model results over a range of the biological parameters describing the mechanistic interactions (equations (2.1)–(2.5)). As we employ a mechanistic description of the feeding interactions with a set of physiological and individual specific parameters, this methodology is a simple way to account for both species and trait diversity, as well as for the uncertain nature of the ecosystems when subject to seasonality and year-to-year variability. The Monte Carlo procedure draws a random set of parameters from a uniform distribution assigned around the values of each mechanistic parameter ±25%. Because of the computational cost of solving the visual range (equation (2.4)), those parameters are not included in the procedure and the value of $\bar{r}_{ij}$ calculated for each data point is treated as a parameter. The Monte Carlo simulations are performed for each month of 4 years (2003–2006), using 500 random parameter sets in each realization. We then calculate the viability of fish and jellyfish in each grid point by counting the event of positive values for forage fish ($F^* > 0$) and jellyfish ($J^* > 0$) groups over the total number of random sets ($N_{\mathrm{tot}} = 24\,000$). From these probabilities, we calculate in each grid point the Ecosystem Susceptibility Index (ESI):

$$\mathrm{ESI} = (p(J^* > 0) - p(F^* > 0)) \times 100. \tag{2.6}$$

This index measures the probabilities of the different food web configurations, and it takes values between ESI = 100 when the model never predicts a viable forage fish population (while jellyfish are present, figure 1*c*) and ESI = −100 when forage fish are always present and no jellyfish can be sustained in the food web (figure 1*b*). An index value around zero generally means that fish and jellyfish are present with equal probability. Alternatively, it can also arise from not having either, but in our application this case is rare. The index is a measure of how much the environment favours the jellyfish over the fish, and accounts for the sensitivity of the food web towards perturbations in environment or species composition that might push the system towards jellyfish domination.

(d) Model forcing

The model is forced with satellite data on primary production (R), light availability (I) and light attenuation coefficient (K_d).

Primary production R consists of 4 years (2003–2006) of monthly averaged data (mg C m^{-2} d^{-1}; [36]), and we assume that these values are representative of the production in the upper (0-$Z_{\max}$) layer.

A climatology of monthly average solar radiation (Watt m^{-2}; [37]) is used to calculate the irradiance (µE photons m^{-2} s^{-1}) in equation (2.3) by applying a conversion factor accounting for the visible fraction and daylight length. Four years of global data (2003–2006) on light extinction coefficient from satellite observations [38] are used to assign the values of K_d in equation (2.3).

(e) Temperature effect

Several studies have indicated that vital rates like respiration, pulsation frequency or growth rate of locally adapted jellyfish are often unaffected by temperature [39,40]. By contrast, respiration rates of local fish and copepods are affected by latitudinal ambient

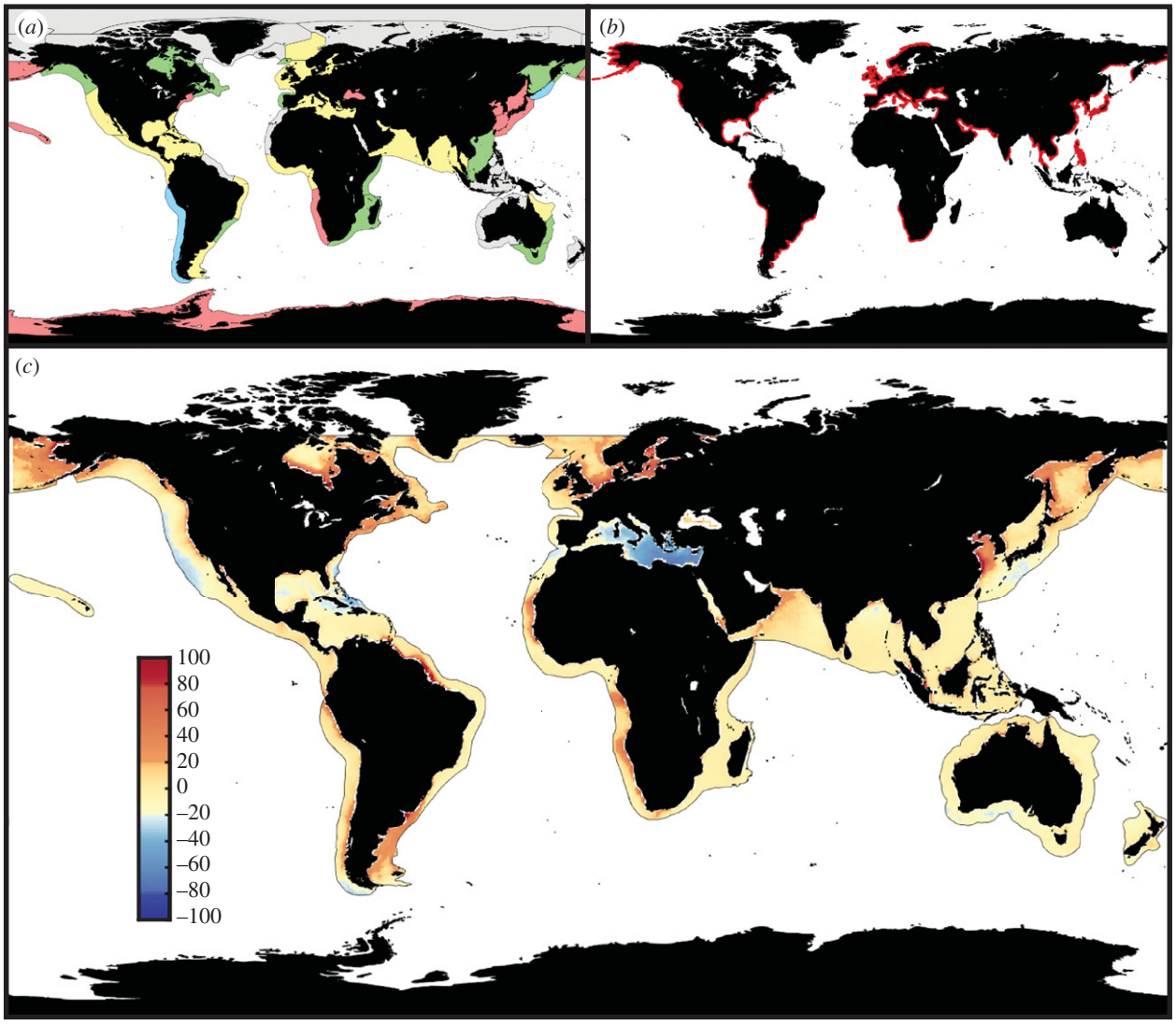

Figure 2. (*a*) Trends in jellyfish populations in the Large Marine Ecosystems (reproduced with permission from [14]). Colours represent areas with increasing trends and low uncertainty (red), increasing trend and high uncertainty (yellow), stable or fluctuating biomass (green), decreasing trend (blue) or no data (grey). (*b*) Global occurrences of coastal jellyfish blooms (red lines; reproduced with permission from [3]). (*c*) ESI for the Large Marine Ecosystems, as generated by our model. Positive values indicate that jellyfish are more likely to be present than forage fish, negative numbers the opposite.

temperature differences [41,42]. Thus, we investigate the effect of temperature on the results when we apply a Q_{10} of 1.8 [41,42] on the respiration rates of fish and copepods (m_{Z_s}, m_{Z_l}, m_F and m_P in equation (2.1)), e.g. $m_{F.25^\circ C} = m_{F.15^\circ C}\ 1.8^{(25^\circ C - 15^\circ C)/10}$, and then calculate the change in ESI relative to a reference temperature value of 15°C, e.g. $\Delta ESI = ESI_{25^\circ C} - ESI_{15^\circ C}$. Note that generally temperature is also expected to affect growth rates via increased activity, however, it is difficult to apply the same scaling on growth rates within the specific mechanistic formulation on feeding rates used in our model. Indeed, we lack information on how temperature affects fish swimming speed, prey capture and sensing and hence, as we can only account for the effect of temperature on respiration rates of fish and copepods, we do not use temperature effects in our global simulations, but instead investigate the sensitivity of our estimated ESI to this important factor.

3. Results

(a) Global results

The model predicts distinct patterns in the ESI (figure 2*c*), with high probability of coexistence of forage fish and jellyfish in most areas (electronic supplementary material, figure S6). Higher ESI occurs in regions with high levels of primary production, especially in areas that are also close to major watersheds and consequently have high turbidity, e.g. in the Baltic Sea and more generally in several coastal areas (such as in the Benguela current, Patagonian shelf and East China Sea). By contrast, we observe low scores in oligotrophic regions (e.g. in the eastern Mediterranean). Surface irradiance does not seem to have a very large impact on the generated patterns.

Few regions are strongly dominated by either fish or jellyfish ($ESI < -80$ or $ESI > 80$). Instead, most areas of the LMEs have ESI scores in the −20 to +20 range, meaning that coexistence of fish and jellyfish is predicted. Regions where neither fish nor jellyfish are predicted are rare (electronic supplementary material, figure S6*a*). Hence, environmental perturbations that can affect the competitive interactions in the model (whether natural or anthropogenic) are not expected to significantly change the food web structure in those areas. Other regions are predicted to favour either fish or jellyfish to a moderate extent ($-80 < ESI < -20$ or $20 < ESI < 80$). These areas are the ones predicted to be sensitive to environmental perturbations affecting the competitive interaction between fish and jellyfish, and include the California,

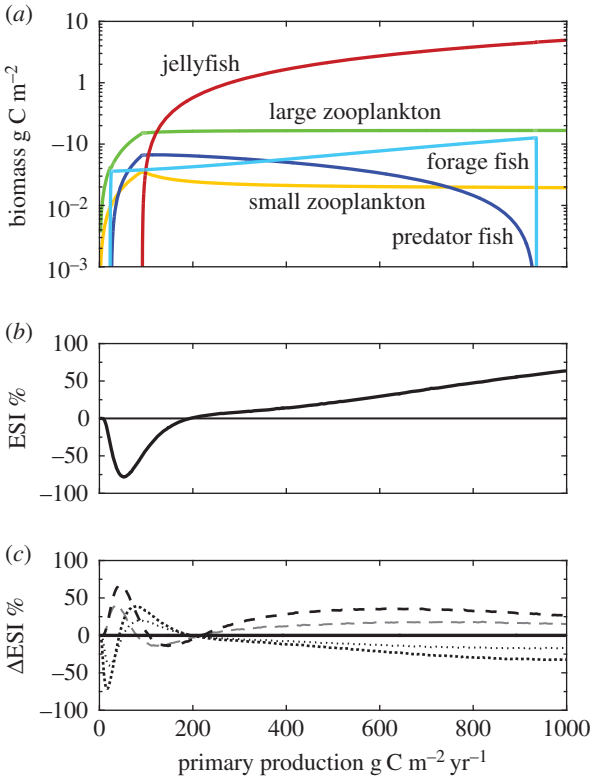

Figure 3. Food web structure at increasing primary production. (*a*) Equilibrium biomasses of predator fish (blue), forage fish (light blue), jellyfish (red), large zooplankton (green) and small (yellow) zooplankton, at increasing primary production, and fishing mortalities (y_F and y_P) of 0.5 yr^{-1}. (*b*) Values of ESI at increasing primary production, using a total of 500 random parameter sets. (*c*) ESI anomaly at different temperatures and primary production. The anomaly is the difference between ESI values at 25°C (dashed dark line), 20°C (dashed grey line), 10°C (dotted grey line), 5°C (dotted dark line) and the reference ESI at 15°C. For this figure, we assume a relationship between primary production and light attenuation $K_d = 3.257 \times 10^{-9} \times R + 0.05952$, based on regression of our satellite data on R and K_d (bootstrap method, $p < 0.001$, $R^2 = 0.1537$).

Humboldt and Benguela current systems, as well as the East Bering, Baltic and eastern US continental shelf seas and the Gulf of Oman.

(b) Community structure

The global patterns can be understood by looking at the equilibrium of the model for changes of primary production and fishing mortalities. The model shows a succession of species invasions with increasing primary production and light attenuation (figure 3*a*). At low production, R, only the zooplankton trophic level can be sustained in the food web, while successive higher trophic levels can be present as primary production increases. The model predicts that forage fish populations are sustainable when primary production is $R > \sim 30$ g C m^{-2} yr^{-1}, with predator fish entering the system almost immediately after this threshold, i.e. when the forage fish biomass is $F^* \approx 3.5 \times 10^{-2}$ g C m^{-2}. The forage fish is then controlled by the predator and both fish groups, as well as zooplankton, increase until jellyfish can enter the system, at $R \approx 90$ g C m^{-2} yr^{-1}. The biomass of jellyfish exceeds that of their forage fish competitors at $R > \sim 100$ g C m^{-2} yr^{-1}, and thereafter increases linearly with primary production.

There is a large range of R in which all groups can be present in the food web, and where jellyfish generally dominate

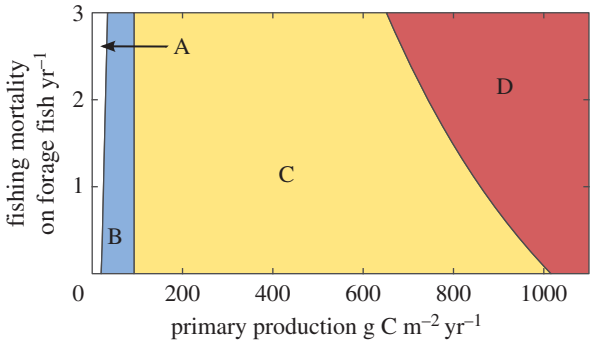

Figure 4. Regions of coexistence at different values of primary production and forage fish fishing mortality. For any given point, the model predicts the presence of neither fish nor jellyfish (A), the presence of fish but not jellyfish (B), coexistence of both fish and jellyfish (C) or jellyfish only (D). The threshold of forage fish entry is sensitive towards fishing, whereas the jellyfish entry threshold is not.

the biomass. This is the region where ESI ≈ 0 (figure 3*b*) and further increases in R in this region increases biomasses of forage fish and jellyfish, but not predator fish. This is due to decreases in fish visual range caused by the increased turbidity associated with high R, in combination with the competition from jellyfish. The gradual decrease in predation pressure allows forage fish to increase initially, but the effects of decreased light availability and competition eventually cause the extinction of the fish (F and P) from the food web, at $R \approx 930$ g C m^{-2} yr^{-1}. In the absence of jellyfish, fish are present over the entire range of primary production even with values as high as 2000 g C m^{-2} yr^{-1}. It is the combined effects of erosion of fish feeding ability and the competition with jellyfish for zooplankton that can drive fish to extinction.

The ESI score is affected by temperature changes (figure 3*c*). As temperature increases, respiration of fish increases, and more zooplankton is needed to sustain forage fish, thus changing the threshold values of primary production for fish entry and extinction (figure 3*a*). Thus, with our simple description of temperature effects, we obtain that the direction of ESI change with changes in temperature depends on the level of primary production, but that for most primary production values, ESI increases with increasing temperature, and *vice versa*.

These results are robust to changes in fishing pressure on forage fish (y_F, equation (2.1)), although thresholds for the entry and eventual elimination of fish from the food web are shifted, so that the region of R where fish thrive expands (contracts) with decreasing (increasing) fishing mortality on forage fish. Thus, both fishing mortality and primary production can drive changes in the model food web structure, and four distinct coexistence regions can be identified (figure 4): an extremely oligotrophic region where fish cannot be sustained (figure 4A), a moderately oligotrophic region that supports fish but not jellyfish (figure 4B), a large intermediate region with coexistence of fish and jellyfish (figure 4C) and a eutrophic region where fish are competitively excluded and jellyfish are present (figure 4D). Transition from state B to C does not depend on fishing mortality on the forage fish. This is because in this region fishing mortality mainly has an impact in regulating the abundance of the top predator as in all predator–prey systems of this kind. In the absence of the predator fish, this transition will depend on the level of fishing mortality. Moreover, increasing fishing mortality always

regulates the extent of the coexistence regions (figure 4) and, in general, the structure of the food web depends on a nonlinear relationship between fishing mortality and primary production. Hence it is difficult to identify the importance and thresholds of these drivers when taken in isolation.

4. Discussion

We show that high productivity and trophic control, in combination with fishing pressure and reduced water clarity can combine to drive a simple ecosystem towards increased jellyfish biomass and eventually competitive exclusion of the (forage) fish. At low and intermediate levels of primary production and turbidity, and for a large range of the parameter values, the occurrence of large increases in jellyfish populations and competitive exclusion of fish are unlikely in our model. Indeed, over a wide range of parameters, coexistence of fish and jellyfish (ESI ≈ 0) is quite robust to changes in parameter values that could arise due to, e.g. climate, fishing, species invasion and other environmental change. Even including the drastic effects of temperature in changing the respiration rates of fish and zooplankton, we obtain a variability of ESI within 20% in non-oligotrophic regions, suggesting continued high levels of coexistence in regions where we calculate ESI ≈ 0.

Our descriptions of the feeding interactions are to a large extent based on simple mechanistic descriptions of processes occurring at the individual level. The formulations employed are general for each life form included in the model. However, the specific parameters used in the expressions can be species-specific. For example, fish species have different light sensitivities or swimming speeds, and all zooplankton species are not equal in size or conspicuousness. The Monte Carlo method employed swipes over a large range of species-specific parameters, making our results robust to changes in the species composition.

Therefore, in regions where our idealized food web is representative of real conditions, we predict that drastic jellyfish outbreaks and ecosystem takeovers are unlikely to occur at low and intermediate productivity, although localized blooms are possible. On the contrary, in highly productive eutrophic regions, especially those influenced by terrestrial run-off, we predict that jellyfish are not only more likely to occur, but also that small perturbations and increased fishing are more likely to push ecosystems towards jellyfish dominance and forage fish crashes. This is important because these are also the regions that support the largest net-based fisheries in the world [3].

Jellyfish population sizes are highly variable in both time and space, due to the ability of jellyfish to aggregate (e.g. [43]) and respond rapidly to favourable conditions [9]. The ESI (figure 2*c*) should not be interpreted as a measure of relative abundance, but rather as an indicator of the vulnerability of the ecosystem to perturbations that may favour jellyfish populations overall or promote local blooms. Note that high ESI does not mean that an area is in fact dominated by jellyfish, but rather that the equilibrium between fish and jellyfish is more vulnerable to changes in environmental conditions that may lead to jellyfish dominance. Likewise, intermediate ESI scores in very oligotrophic environments reflect the absence of both jellyfish and fish (electronic supplementary material, figure S6), and those regions would at least initially become fish dominated if primary production were to increase. In spite of these reservations, it is nevertheless relevant to compare the global patterns in ESI to observations of jellyfish.

Recently, a few studies have investigated jellyfish patterns on a global level [3,14,15]. Of these, Lucas *et al*. [15] used available data to assemble global biomass maps of jellyfish, showing that ctenophores and cnidarians are ubiquitous in the world's oceans. Robinson *et al*. [3] presented data on jellyfish bloom occurrence and their adverse effects on fisheries to show that there is considerable overlap between the world's largest fisheries and coastal jellyfish blooms (figure 2*b*). Finally, Brotz *et al*. [14] used various sources of information to detect trends in jellyfish populations in coastal ecosystems (figure 2*a*).

A qualitative comparison between the ESI and the jellyfish population trends (figure 2*a*) and frequent blooms of jellyfish (figure 2*b*) reveals an overall good correspondence. Almost all LMES where jellyfish have been increasing (figure 2*a*), have areas with high ESI (figure 2*c*), with the exceptions of northeast Australia and the Mediterranean Sea. Similarly, bloom occurrences (figure 2*b*) also largely correspond to regions with high ESI, again except for the Mediterranean Sea. We note that in the Mediterranean Sea, our model is likely missing some fundamental processes (e.g. hydrographical features or temperature effects) as this is a region where jellyfish blooms are often reported, even though primary production is low.

Temperature is important for the life history of many (especially cnidarian) jellyfish [16]. As an example, the timing and magnitude of the release of scyphozoan ephyrae from benthic polyps is highly temperature dependent in many cases [16,31]. However, the direction and magnitude of this temperature effect on life history is variable between organisms and areas [16,31], and in addition, our model is not able to capture life history and ontogenetic growth.

In our model, ESI generally increases with increasing temperature (figure 3*b*) and decreases with decreasing temperature, although the magnitude and direction of this change is dependent on the level of primary production and light attenuation. Other studies have found a link between increased temperature and jellyfish proliferations in some cases [16,44], and the lack of this driver in our global model may account for some of the discrepancy between model results and observations. Temperature change may partially explain the mismatch in the oligotrophic eastern Mediterranean Sea, because it can produce large changes in food web structure in oligotrophic regions in our model (figure 3*c*).

Despite the very simplified structure of our model and the limits in the number of processes that we can resolve, the ESI score appears to compare generally well with available observations—which are themselves not perfect. Moreover, the predictions of zooplankton, fish and jellyfish biomasses are consistent with those reported by Oguz & Gilbert [7] using long time series in the Black Sea (see the electronic supplementary material, table S5).

Changes in turbidity initially only negatively affects the predator fish (P), while the biomass of forage fish increases. Similarly, fishing mortality on forage fish does not immediately affect forage fish biomass prior to their disappearance, but instead decreases the biomass of their predators. This lack of an immediate biomass response of a prey species is universal to Lotka–Volterra-type models like this one [27].

However, this does not mean that the forage fish are unaffected. Their production does indeed decrease, but this is compensated by a decrease in the predator biomass. When we run the model without predator fish, forage fish biomass does indeed decrease with increasing fishing mortality, and we would argue that overfishing on forage fish often occurs after the depletion of predatory fish stocks, i.e. 'fishing down the food web' [8,45]. Trophic control on forage fish is a key feature in our model and is supported by many observations of trophic cascades in fish ecosystems [7,8,46,47]. Moreover, the predicted sudden replacement of fish by jellyfish when this trophic control breaks is similar to what has been observed in some systems [6,8].

Jellyfish predation on the younger stages of fish is an important process in many systems, whereas there is little evidence of the opposite [3]. Most large, blooming jellyfish prey on fish eggs and/or larvae to some extent, although the magnitude of this is very variable. Intraguild predation by jellyfish on young stages of forage fish may negatively affect recruitment to the fish stocks in some cases, provided that there is a significant overlap in distributions and timing, as well as sufficiently large abundances of jellyfish. Here, we have focused on competition regulated by the environment and neglected intraguild predation. Hence, our results can be considered conservative, as this process is expected to reinforce the ability of jellyfish to replace fish at high zooplankton densities. However, to properly estimate the relevance of this process in regulating fish dynamics, a different approach using, for example, physiologically structured population models would probably be needed.

A critical assumption in our model is the lack of trophic control on jellyfish. An increasing amount of studies indicate that jellyfish are not exclusively 'dead ends' in the food web, but are in fact predated opportunistically by many predatory fish [25]. However, our model mainly describes large jellyfish that apparently have few specialized predators, but are rather consumed opportunistically (e.g. [25,26]). This results in a weak trophic coupling and in low control of jellyfish biomasses by these predators. Consistent with other studies [3], we assume that jellyfish can have a large impact on lower trophic levels but do not transfer energy further up in the food web very efficiently.

Many important forage fish, such as anchovies, menhaden and sardine are also able to filter-feed [48]. This could potentially cause predation efficiency of forage fish in our model to be underestimated. A forage fish with the carbon weight assumed in our model corresponds to a fish of approximately 8 cm in length and a maximum gape size diameter of 1.19 cm [49]. If we calculate the visual area for the forage fish feeding on the large zooplankton, we get a diameter minimum of 1.25 cm (0.72 cm for the small zooplankton). We conclude that including filter feeding for forage fish in our model would not change the results as minimum visual range is comparable to the gape size.

The interaction between visual feeding and the water turbidity describes a mechanism where bottom up forcing directly affects key traits of organisms at higher trophic levels. This highlights the importance of describing organism traits and not just biomasses in ecosystem models. Models developed on fundamental traits are general, and allow applications across different ecosystems as long as the interactions based on a mechanistic description of proximate factors are still valid. This is particularly important to describe jellyfish ecology across ecosystems, since the lack of long time series of jellyfish populations makes it hard to construct good statistical models of jellyfish populations on a global scale.

Mechanistic models of the relative profitability of jellyfish and fish feeding modes have been studied before [23], and the relationship between system production and turbidity is similar to previous modelling studies for the Baltic Sea [27]. However, to the best of our knowledge, this is the first mechanistic model of fish and jellyfish competition that has been applied on a global scale.

Authors' contributions. All authors contributed in conceiving the study. N.A.S.-M. performed modelling work, with the help of P.M. N.A.S.-M. and P.M. collected data. N.A.S.-M., P.M. and T.K. analysed model output. N.A.S.-M. wrote the first draft of the manuscript, and all authors contributed substantially to revisions. The solutions of the model equilibria are available upon request to the main author.

Competing interests. We have no competing interests.

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Supplementary Information:

Table S1. Global parameters used in the model.

Symbol	Variable or parameter	Unit	Value	Source
f	assimilation efficiency	-	0.75	
c	beam attenuation coefficient	m^{-1}	0.4	[1,2]
K_d	total diffusive light attenuation	m^{-1}	-	
I	light intensity just below the surface	$\mu E\ m^{-2}\ s^{-1}$	375	
K_e	visual half-saturation constant	$\mu E\ m^{-2}\ s^{-1}$	5	[3]
Z_{max}	integration depth	m	70	
d	light part of the day	-	0.6	
z	productivity of small zooplankton relative to large	-	0.1	Based on clearance rates
T_Z	primary:zooplankton production transfer efficiency	-	0.1	[4]
ϑ	reaction field half angle	degrees	20	
S	jellyfish filtration efficiency	-	0.89	[5]
$A_{F.Zl}$	capture probability of forage fish on large zooplankton	-	0.5	
$A_{F.Zs}$	capture probability of forage fish on small zooplankton	-	0.75	
$A_{C.F}$	capture probability of predator fish on forage fish	-	0.06	
L_j	jellyfish diameter	m	0.12	[6]
R	Primary production	$g\ C\ m^{-2}\ y^{-1}$	-	
Q_{10}	Q_{10} value for fish and copepod respiration	-	1.8	[7,8]

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Table S2. Species-specific parameters used in the model.

Symbol	Variable or Parameter	Unit	C	F	J	Zl	Zs	R	Source
C	contrast	-		0.8		0.6	0.5		
δ	natural mortality	y^{-1}	3.7		3.7				[9,10]
m	respiration	d^{-1}	3.5E-03	1.3E-02	3.06E-02	0.15	0.071		[11]
a	image area	m^2		2.3E-04		2.4E-07	4.7E-08		calc. from carbon assuming prolate spherical shape
w	carbon weight	g C ind^{-1}	100	0.5	0.1	4E-06	4E-07	1E-9	
v	swimming speed	m s^{-1}	0.55	0.20	2.5E-02	1.6E-03	7.3E-04		[12–14]
E	eye sensitivity parameter	-	1.1E+05	7.6E+04					[15]
Y	Fishing mortality	y^{-1}	0-0.5	0-3					

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Figure S3. Comparison of model jellyfish clearance rates with observations.

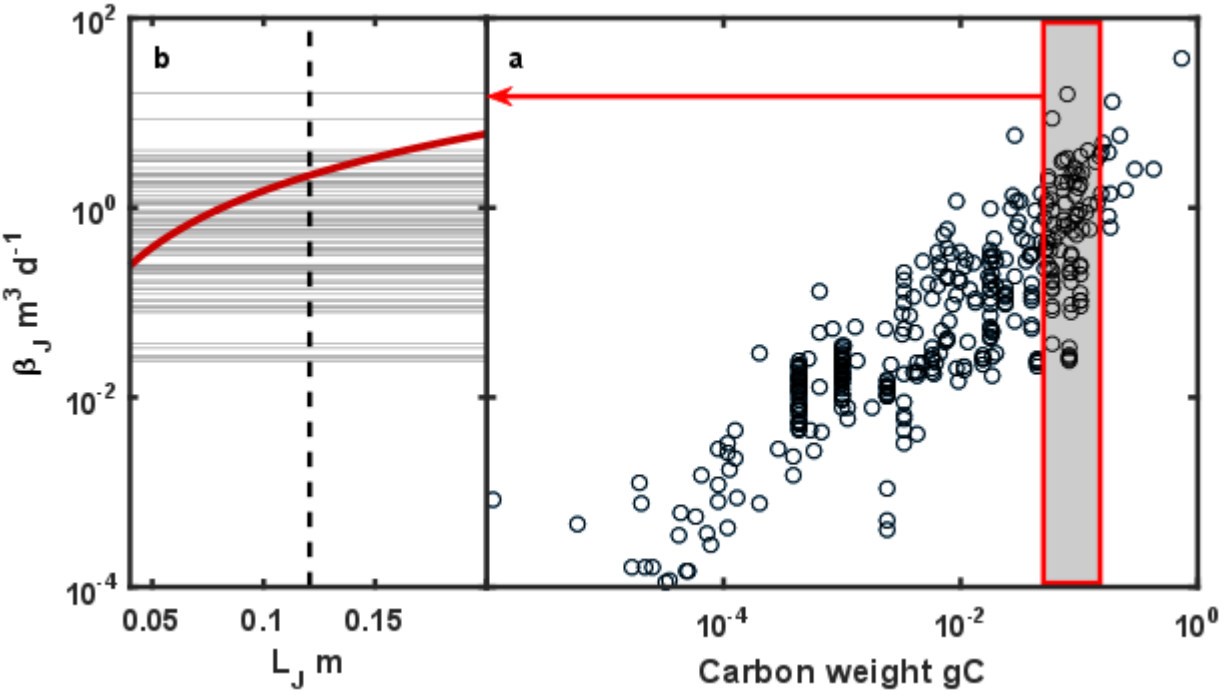

Figure S1. a: Observations of clearance rate β_J vs carbon weight for jellyfish from [5]. The red square contains observations of clearance rates of jellyfish with the same size as in our model ± 50%. b: Clearance rate of jellyfish as a function of jellyfish diameter L_J (red line), as calculated by our model (Eq. 6). L_J is the most sensitive parameter for jellyfish clearance rate (calculated as change in clearance rate relative to change in parameter). Grey horizontal lines are the observations of jellyfish clearance rate from within the red square in panel a. Dashed vertical line is the default value of parameter L_J in our model.

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Figure S4. Comparison of model fish clearance rates with observations.

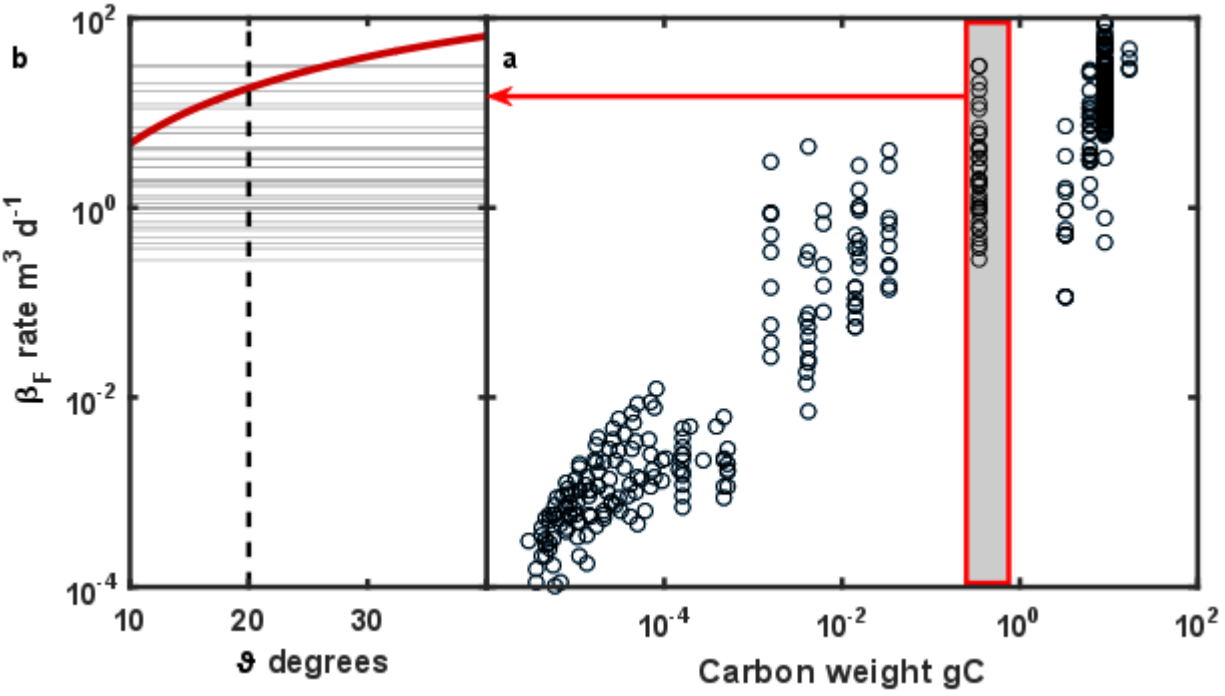

Figure S2. a: Observations of clearance rate β_F vs carbon weight for fish from [5]. The red square contains observations of clearance rates of fish with the same size as in our model ± 50%. b: Clearance rate of fish as a function of fish reaction field half angle ϑ (red line), as calculated by our model (Eq. 6). ϑ is the most sensitive parameter for fish clearance rate (calculated as change in clearance rate relative to change in parameter). Grey horizontal lines are the observations of fish clearance rate from within the red square in panel a. Dashed vertical line is the default value of ϑ in the model.

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Table S5. Comparison between biomasses of fish, jellyfish and zooplankton from the interior basin of the Black Sea, and biomasses predicted by our model.

Species	Oguz and Gilbert [16], reported value (unit)	Oguz and Gilbert [16], converted values (g C m^{-2})	Model predictions (g C m^{-2})
Jellyfish	0-3.5 (kg m^{-2})	0-4.8*	0-5
Forage fish	100-1100 (kt)	0.025-0.28†	0-0.15
Predator Fish	-	-	0-0.06
Zooplankton	2-20 (g m^{-2})	0.2-2‡	0-0.2

*Assuming carbon:WW ratio of 1.4e-3. †Assuming carbon is 10 % of WW, and area of the Black Sea interior Basin is 400,000 km^2. ‡ Assuming carbon content is 10 % of WW.

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Figure S6. Maps of the individual model outcomes synthesized in the Ecosystem Susceptibility Index (ESI, see main section 2.3).

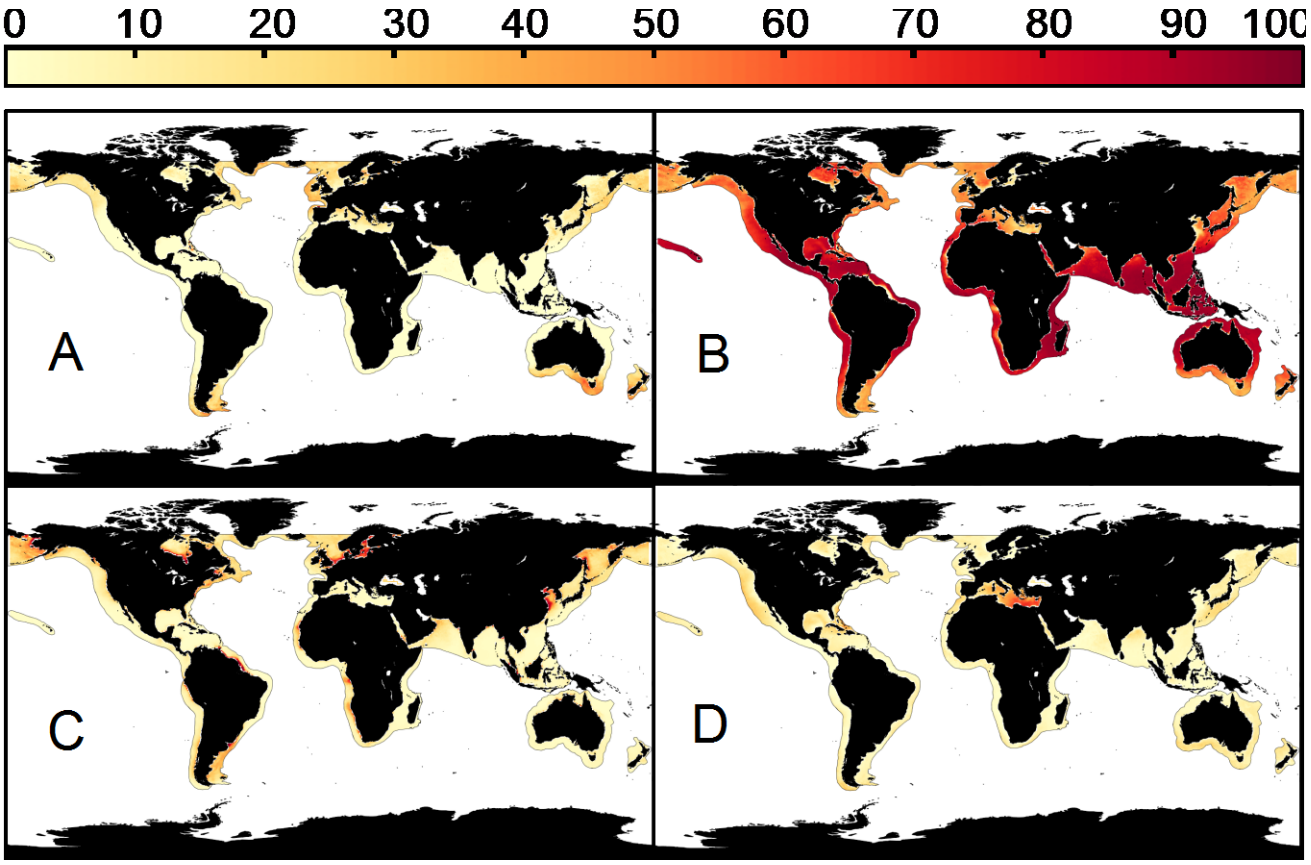

Figure S4. A: Percentage of Monte Carlo runs resulting in neither fish nor jellyfish. B: Percentage of Monte Carlo runs resulting in coexistence of fish and jellyfish. C: Percentage of Monte Carlo runs resulting in jellyfish, but not fish. D: Percentage of Monte Carlo runs resulting in fish but not jellyfish.

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Chapter 4. **Manuscript II**

Boom and Bust: Life history, environmental noise, and the (un)-predictability of jellyfish blooms

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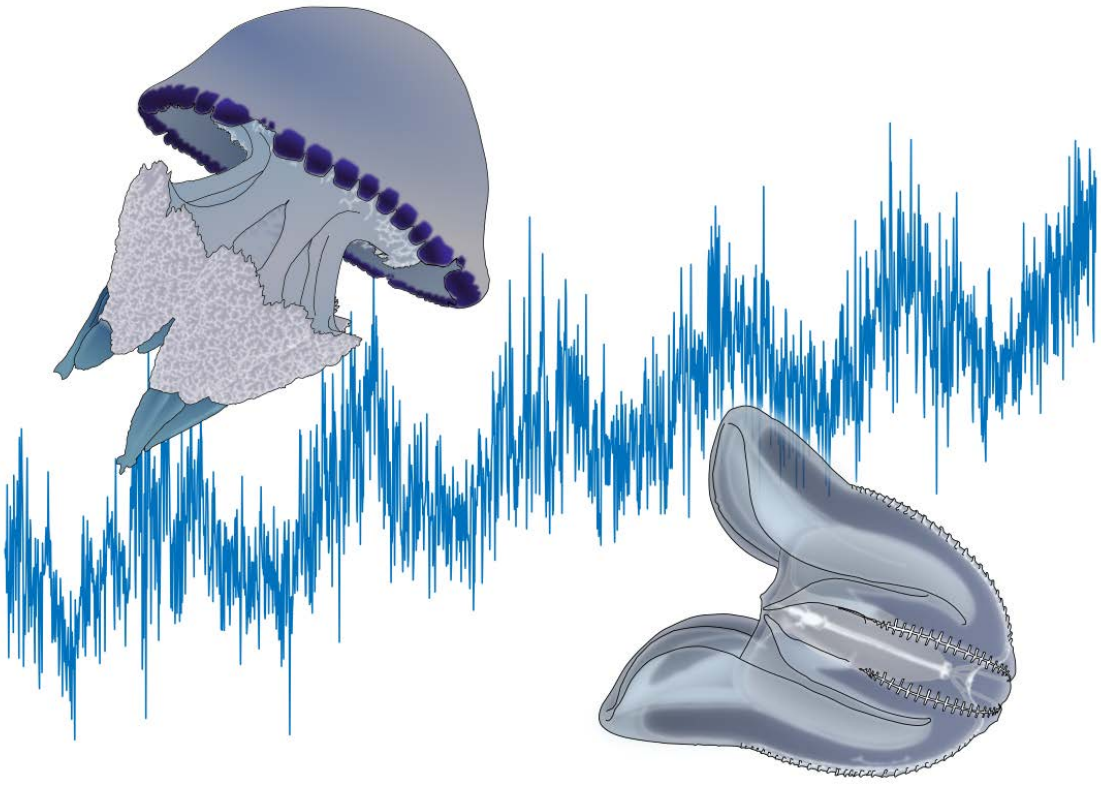

Abstract

Jellyfish (pelagic Cnidarians and Ctenophores) form erratic and seemingly unpredictable blooms with often large, transient effects on ecosystem structure. To rapidly capitalize on favorable conditions, jellyfish can employ different life histories, which are either a life cycle with one annual sexual reproduction event and an overwintering benthic stage (metagenic life cycle), or continuous reproduction and a holoplanktonic life cycle. However, the links between life history, blooms, and environmental variability are unclear.

Here, we examine how environmental variability can drive the bloom dynamics of different jellyfish life histories in coastal ecosystems. With a simple community model, we reproduce typical temperate seasonalities of the two strategies and trophic cascades triggered by abundant jellyfish, demonstrating how erratic blooms can be generated by irregular changes in the environment. Consistent with observations, we predict that metagenic jellyfish dominate early in the season, compared to holoplanktonic organisms, and are favored by increased seasonality. Our results reveal possible mechanisms driving coastal patterns of jellyfish blooms, and factors that are important for the outcome of competition between jellyfish with different life cycles. Such knowledge is important for our understanding of jellyfish blooms, which have large consequences for human activities and well-being, and may improve our ability to predict and manage local ecosystems.

Keywords

Population dynamics, life cycle, reproductive strategies, environmental drivers, water exchange, advection, coastal ecosystems, trait based model, seasonality

Introduction

Jellyfish outbreaks are widely recognized for their variable and unpredictable dynamics, with individuals suddenly appearing in large numbers, only to later be seemingly absent from the ecosystem(1). Such fluctuations typically have a seasonal component at temperate latitudes, but there is also important variation on interannual or longer time scales(2). Much attention has been given to these erratic jellyfish blooms, because of their often drastic consequences for local or regional ecosystem structure and functioning(3–5). Most bloom-forming jellyfish are efficient predators of zooplankton(6), and may effectively control grazer populations when abundant(7–11). This in turn releases primary producers from predation control, eliciting phytoplankton blooms(5) and favoring jellyfish in the competition with fish(12–14). Such trophic cascades can be self-reinforcing, because phytoplankton blooms often lead to oxygen depletion in coastal waters, stimulating nutrient release from the bottom and further algal growth.

Though our understanding of their causality is limited, the tendency of some jellyfish to form massive blooms must be linked to a combination of their environment, its variability, and their traits(6, 15). True jellyfish blooms caused by local population growth, as opposed to aggregation from other areas, often occur in coastal enclosed or semi-enclosed environments like marine lakes, lagoons, fiords, estuaries and bays(16–20). In such areas, where advective loss of the slow-swimming jellyfish is low and production high, spectacular abundances may occur, often leading to population regulation through density dependent effects(21, 22). Whether blooms occur seasonally or seemingly at random, they emerge and disappear in response to changes in environmental conditions. Thus, the occurrence of blooms is linked to the magnitude and patterns of fluctuations in environmental variables such as advective displacement, temperature or salinity.

Whereas jellyfish blooms require suitable environmental conditions to occur, the ability of jellyfish to quickly respond to changes in those conditions depend on specific traits promoting high growth and reproductive rates (23). While their simple body plans can support rapid growth, they also limit their ability to cope with food shortages. Broadly speaking, jellyfish generally employ one of two different life history strategies to cope with environmental fluctuations, being either metagenic or holoplanktonic (1).

Metagenic jellyfish maintain themselves through adverse periods in a benthic life stage that can reseed the population when favorable conditions return. This strategy is typical of scyphozoan cnidarians, which contain the majority of bloom forming species(6, 15). Most scyphozoans have an asexually reproducing polyp stage that releases one or more ephyrae (small medusae) into the water column at the onset of the productive season(24). These ephyrae grow into adult medusae that reproduce sexually, producing small planula larvae that in turn settle as polyps(24).

Holoplanktonic jellyfish instead have plastic life histories, going through boom and bust cycles and relying on some adults to survive through the bad season to quickly capitalize on renewed resources. This is typical of lobate ctenophores, which are hermaphroditic, self-fertilizing, and able to produce offspring as juveniles, giving them short generation times(25, 26).

Both these reproductive strategies have trade-offs. For example, the polyps of metagenic jellyfish may ensure their continuity during adverse periods, may increase asexually providing a buffer against recruitment failure, and may provide the metagenic jellyfish with a head start at the beginning of the season. However, they are also dependent on suitable polyp substrate, and are vulnerable to adult mortality because they cannot replenish in the water column. Conversely, holoplanktonic jellyfish populations depend on the number of individuals left after a period of adverse conditions, but can reproduce continuously, allowing them to recover from mortality events during the growth season. Thus, both strategies enable jellyfish to take advantage of transient favorable conditions, but are not equal in their advantages and disadvantages. Hence, it is interesting to investigate if and how trade-offs in the different life history strategies can interplay with environmental variability to favor one or the other.

Here, in light of the above, we aim to investigate the erratic nature of some jellyfish blooms, and to explore the relative success of the two main life history strategies of jellyfish. We examine whether different types of environmental variation in advective loss can produce bloom dynamics similar to those in nature, and how the two life history strategies perform under different scenarios of advective loss and polyp habitat availability. We address these questions by introducing a relatively simple food web model containing jellyfish with the two different reproductive strategies, exposed to seasonal phytoplankton dynamics and realistically fluctuating levels of water exchange (Figure 1).

Methods

Model system

We model the seasonal cycle of dissolved inorganic nitrogen N, phytoplankton P, zooplankton Z, detritus D, metagenic jellyfish M and holoplanktonic jellyfish H as a chemostat-type system with the common currency of nitrogen (mmol m^{-3}). The model system interacts with surrounding water masses through a water exchange rate Δ, flushing the system with water containing outside concentrations of nitrogen, phytoplankton and zooplankton (N_i, P_i and Z_i, respectively), and transporting jellyfish

out of the system (Figure 1). Whereas all other populations are described as single state variables in units of nitrogen concentration, metagenic jellyfish biomass is resolved into individual jellyfish nitrogen content (M_w), and abundance (M_a), thus resolving individual and population growth.

Nitrogen dynamics are the sum of water exchange, higher trophic level excretion, remineralization of detritus and phytoplankton uptake, with phytoplankton nitrogen uptake modelled with a Michaelis-Menten formulation. The zooplankton grazes the phytoplankton following a Holling type III functional response which is typical for a coastal copepod such as Acartia spp.(27), and is removed through mortality, respiration and jellyfish predation. Sinking phytoplankton and unassimilated jellyfish and zooplankton food go into the detritus, which is remineralized back into the nitrogen pool.

While jellyfish clearance rates are typically constant for (realistic) prey concentrations(28–30), their growth rates do saturate, as surplus ingestion is regurgitated(31). Thus, whereas both types of jellyfish remove zooplankton with a linear (Holling type I) functional response, the prey is assimilated with a saturating (Holling type II) functional response, with surplus ingestion going to detritus. For both jellyfish, biomass is lost through mortality, respiration and water exchange.

A new generation of metagenic jellyfish ephyrae (E, ind. M^{-3}) are released once a year (March 1st), describing a typical phenology for *Aurelia aurita* (24). This initial abundance cannot increase during the course of a season, but decreases through advection and mortality. Any remaining biomass at the end of the season (November 1st) is moved to the detritus pool. This resets M_a and M_w to zero in the model, before a new cohort is added next spring.

The factors controlling maturation and reproductive allocation in adult metagenic jellyfish are not well understood, but are plastic with respect to size and seem related to food availability and age(32). Additionally, Miyake et al. (33) found that gonad maturity of *Aurelia aurita* accelerated with age. In our model, reproductive allocation starts at a low value in summer (July 1st), and then increases linearly to a given maximum value (ω) later in the season. We do not resolve polyp population dynamics, but rather assume independence between planula and ephyrae production. At any rate, the vast majority of planulae and polyps will perish, and consequently the production of planulae goes into to the detritus in the model.

A detailed description of all model equations can be found together with a table of parameter values (Table S1) in appendix S1.

Seasonality

Seasonal dynamics in the model are forced through seasonal fluctuations in temperature and phytoplankton growth rate. Temperature affects growth, respiration, clearance, and remineralization in the model according to their respective Q_{10} values.

Seasonal concentrations of nitrogen, phytoplankton and zooplankton in the incoming water (N_i, P_i and Z_i) are calculated by running the model without jellyfish, zero water exchange ($\Delta = 0$), and a total nitrogen pool ($N + P + Z + D$) equal to 70 mmol N m^{-3}. The resulting seasonal concentrations of nitrogen, phytoplankton and zooplankton were then used as input for model runs including jellyfish. Under these conditions, the model reaches a steady seasonal cycle with a classical spring phytoplankton bloom followed by zooplankton increases in summer.

Water exchange rate

Depending on the region, the exchanges between local and surrounding areas can occur at different intensities and at several temporal scales, being described by random uncorrelated fluctuations or more correlated dynamics including seasonal patterns. In our model we simulate water exchanges as

$$\Delta(t) = \bar{\Delta} \times \mathrm{A} \sin\left(\frac{2\pi}{365} t - \varphi_{\Delta}\right) \times \varepsilon(t) \ , \qquad (1)$$

where $\bar{\Delta}$ is the average water exchange rate, A is the amplitude, φ_{Δ} is the time of seasonal maximum, and $\varepsilon(t)$ is some random environmental noise at time t. The time series generated by the formulation above can represent seasonal as well as random signals, depending on values of ε and A. Δ is assumed to be larger in winter and lower in summer, corresponding to examples of water exchange from real systems(12, 34).

It is expected that environmental noise is autocorrelated in time(35). This can be described by the spectrum of various frequencies that make up the signal in Eq. 1. Natural noise signals often conform to a power law, where the amount of variance contributed by different frequencies scales with frequency v as $1/v^{\Upsilon}$, increasing autocorrelation as Υ increases(35). The noise is said to be 'white' when the spectral exponent Υ is close to zero and 'red' for $\Upsilon \approx 1$, while 'brown' noise has Υ values around 2 (35). Thus, the random noise signal at time t is calculated as(36):

$$\varepsilon(t) = \sum_{v=1}^{t_{end}/2} \frac{1}{v^{\Upsilon/2}} \sin\left(\frac{2\pi v t}{t_{end}} + \theta(v)\right) \ , \qquad (2)$$

where t_{end} is the length of the generated time series and ϑ is a vector of random phases, drawn from the uniform distribution between $[0,2\pi]$. The generated noise is then

normalized to unit maximum amplitude by dividing the noise time series by its maximum absolute, before being applied to Δ.

Code availability

The MATLAB model code is available upon request to the first author.

Results

Seasonal cycle

The model reproduces the main features of a typical temperate seasonal cycle, with a phytoplankton bloom in the early spring followed by increased zooplankton biomass (Figure 2). In the absence of predators, zooplankton controls phytoplankton during summer, while both are low in late winter before the onset of the next season.

The numbers of metagenic jellyfish (M_a) decline rapidly through mortality and advective loss after their introduction in early spring, but the total biomass (M) increases due to growth in individual size. At low values of water exchange (Δ), medusae can maintain relatively high abundances through summer, resulting in density dependence and stunted individual growth (Table 1). Conversely, higher values of Δ result in lower biomass and abundance but larger individual size. After an early summer peak, metagenic jellyfish biomass decreases due to both loss of individuals and increased allocation into reproductive output.

Similarly, the biomass of holoplanktonic jellyfish increases in spring following increases in zooplankton biomass, but typically with a later peak than M, especially when winter Δ has been high (Figure 2). Moreover, whereas the initial spring biomass of metagenic jellyfish only depends on substrate availability (assumed to be constant in the model), holoplanktonic jellyfish depend on the biomass left after the winter.

Interannual variability

Variation in Δ introduces interannual variations in both jellyfish populations, with high biomasses of jellyfish in years of relatively low Δ, and vice versa (Figure 2). In years of low Δ, jellyfish are able to control zooplankton biomass, allowing the development of phytoplankton blooms during summer (Figure 2). The interannual variability in biomasses introduced by variation in Δ depends on the amplitude and temporal correlation of the forcing. The Δ variation employed in our model has two components: regular seasonal fluctuations with amplitude A, and random fluctuations with autocorrelation determined by the spectral exponent Υ (noise color). In order to show the effects of these different patterns of variation, we have run 200-year-long simulations,

with different combinations of these parameters. Each run has then been aggregated into a 'climatology', showing the mean and total variation of each biomass (Figure 3). Increasing Υ has the effect of increasing the interannual variation in Δ as the time series of the noise becomes more autocorrelated. Even though the variance, amplitude and mean of Δ is the same for different levels of Υ, the time scale of the fluctuations relative to the time scale of the population dynamics is important for the resulting variation in biomasses. Thus, the year-to-year variation in biomasses is dependent on the color of the variation in Δ (Figure 3, top to bottom). While the average biomasses (lines in Figure 3) remain relatively unchanged, the variation around the mean (shaded areas in Figure 3) increases with increasing Υ.

Conversely to changes in Υ, changes in the seasonal water exchange amplitude (A) affect the average seasonal dynamics (Figure 3, left to right). As A increases, the average Δ increases during the winter, and decreases during the summer. Because metagenic jellyfish only experience summer conditions, their biomass increases with A, while holoplanktonic jellyfish become less successful, experiencing high advective losses during the winter. The relatively low Δ during summer also results in increased frequency and magnitude of summer phytoplankton blooms.

The dependency of holoplanktonic jellyfish on the previous years' biomass causes their biomass to be interannually autocorrelated, even when there is strong interannual variation in the forcing. A linear regression of the current and previous years' maximum seasonal holoplanktonic biomass explains 75 % of the variation, in simulations lasting 200 years (same conditions as in Figure 2). In comparison, the previous year only explains 32 % of next year's metagenic jellyfish biomass in the same simulation.

Effects of average water exchange and substrate availability

We also investigate the effects of the average water exchange rate $\bar{\Delta}$, and of the magnitude of spring ephyrae release E, which can be considered as a proxy for substrate availability and growth conditions for benthic polyps (electronic supplementary information, Figure S1). As already observed, total jellyfish biomass is high at low values of $\bar{\Delta}$. The magnitude of E, however, can control which life cycle strategy will dominate. In particular, for values of $E>25$ ind. m^{-3} metagenic forms will dominate the biomass, whereas we predict holoplanktonic dominance at low ephyrae release values ($E<20$ ind. m^{-3}). Increases in $\bar{\Delta}$ reduces the total biomass, and at very high values of delta (>0.035 d^{-1}) total biomass of jellyfish is close to zero, hence no effects of E can be expected.

Discussion

The main conclusions of the study can be summed up as: 1) A simple model can produce seasonal patterns in biomasses of the main plankton groups that are typical of temperate environments, including trophic cascades triggered by high jellyfish biomasses. 2) Advective loss can be an important driver of jellyfish populations and variation in this driver can produce large interannual fluctuations in jellyfish biomass similar to those observed in nature. 3) Metagenic jellyfish tend to dominate earlier in the season compared to holoplanktonic jellyfish, and the metagenic strategy is favored by increases in the seasonal amplitude of the water exchange rate. 4) Biomasses of holoplanktonic jellyfish are predicted to be more interannually autocorrelated than that of metagenic jellyfish. Below we will discuss each of these predictions and compare them to observations from nature as reported in the literature. Comparison of our findings with observations are made difficult by the fact that few studies have directly investigated the effect of advective loss for jellyfish population dynamics. Most of the available studies concern either *Aurelia* sp. (a metagenic scyphozoan) or *Mnemiopsis leidyi* (a holoplanktonic lobate ctenophore), and so the sample of species with which to compare the present study is low. However, these two species have contrasting strategies, occupy similar niches, and are probably the most widespread and frequently blooming jellyfish in the world.

When jellyfish biomasses are relatively low, the seasonal succession of lower trophic levels in the plankton produced by our model are typical of NPZD models(37), with low biomasses in winter, followed by a spring phytoplankton bloom and subsequently high zooplankton biomass throughout summer (Figure 2). At high jellyfish biomasses however, a trophic cascade results from the suppression of zooplankton through jellyfish predation. This in turn results in relaxation of the grazing pressure on phytoplankton, and a summer phytoplankton bloom is generated (Figures 2 and 3), something we do not observe in the absence of jellyfish. These dynamics are similar to observations from field studies in seasonal bay or fiord environments, where high jellyfish biomasses have also frequently been observed to reduce zooplankton abundance, causing phytoplankton blooms(3, 5, 9, 11, 38–40).

We show that loss of jellyfish from a local population through advective processes (Δ) can be an important driver of jellyfish population size, structure and trait composition (Figures 2, 3 and A1, Table 1). When Δ is small, jellyfish are retained in the system and may grow in size (metagenic jellyfish) or numbers (holoplanktonic jellyfish), leading to large summer jellyfish blooms. Likewise, the predicted effect of higher advective loss is to decrease overall biomass of jellyfish, but also to relax density dependent constraints on individual metagenic jellyfish. We would therefore expect jellyfish populations to be larger in enclosed systems (provided enough prey), but the individual size of metagenic

jellyfish to be smaller, due to density-dependent growth limitation. The occurrence of (persistently) high jellyfish biomasses is a common phenomenon in enclosed or semi-enclosed systems, where advective losses are low(41–43). Such areas are found around the world, from tropical and subtropical marine lakes or lagoons(17, 44), to temperate estuaries and fjords(16, 18–20). In such systems, and similar to our predictions (Table 1), density dependence resulting from high jellyfish abundances is often intense, resulting in stunted growth of metagenic jellyfish(9, 21, 22), and a generally negative relationship between metagenic jellyfish individual size and abundance(9, 32), at least for *Aurelia* sp. Reduced competition with fish due to increased turbidity has also been proposed as a mechanism behind the prevalence of jellyfish blooms in enclosed areas(14, 45, 46), however we propose that retention may be an alternative or additional mechanism behind the pattern, one that indeed may work either contrary to or in concert with the optical mechanisms (see ref. (47) for an interesting example).

When we vary the advective loss of jellyfish around an intermediate value, we can observe erratic interannual fluctuations in biomass that are typical of bloom forming jellyfish (Figure 2 and 3). These fluctuations depend strongly on the color (Υ) of the environmental noise, however: If the time-scale of the driver fluctuations are too short compared to the timescale of the population dynamics, they will essentially integrate over the mean driver value, even if driver variance is large (Figure 3). In nature, the color of environmental noise (e.g. in precipitation or wind patterns) tends to be 'white' ($\Upsilon < 0.5$) in inland environments, and red ($\Upsilon \approx 1$) or brown ($\Upsilon \approx 2$) in coastal and oceanic environments, respectively(35). Thus, the environmental variation in the marine environments where jellyfish blooms occur may partly explain the emergence of such bloom patterns. While we have only imposed variation on the water exchange rate in this study, other environmental drivers, especially temperature, are also important for, e.g., polyp ephyrae production(24) and will vary similarly, potentially promoting erratic blooms in the same fashion as for Δ in our model. Global, regional and local jellyfish populations do exhibit long-term oscillations(2) that correlate with climatic indices or variables(19, 48).

Metagenic jellyfish dominate earlier in the season in our model, compared to the holoplanktonic forms. This dynamic is driven by a combination of the slower build-up of holoplanktonic jellyfish, the often lower biomass of holoplanktonic jellyfish in spring, and the onset and increase of reproduction (which does not contribute to pelagic biomass) in the metagenic jellyfish. Of these, the reproductive output of the metagenic jellyfish accounts for most of their low biomass in autumn, whereas higher holoplanktonic mortality accounts for their slower buildup in spring. Higher mortality is assigned to holoplanktonic jellyfish in the model since their individual size will on average be smaller than that of metagenic jellyfish, due to ongoing reproduction. The jellyfish phenology

predicted by the model (Table 2) is corroborated by many studies comparing seasonal dynamics of metagenic (*Aurelia* sp.) and holoplanktonic jellyfish (mostly *M. leidyi*) in temperate regions(12, 49–52); in these temperate regions, *M. leidyi* consistently blooms later in the season than *Aurelia* sp., though caution should be exercised, since *M. leidyi* is a warm-water adapted species.

Related to the above, the results also suggest that increased seasonality of advection will benefit the metagenic jellyfish (provided Δ peaks during winter). The most important factor for the competitive outcome in the model seems to be the relative biomasses of the two competitors at the start of the growth season. Because the metagenic jellyfish are re-seeded each spring, an important benefit of the metagenic life cycle is to buffer the effects of interannual environmental variability. Thus, we predict that holoplanktonic jellyfish are more vulnerable to year-to-year variation. Although we have not found any studies on the interannual autocorrelation of jellyfish populations, many studies of *M. leidyi* stress the importance of winter conditions and retention for local population persistence(40, 43, 53–55).

Though we have assumed populations in isolation throughout this study, in nature local populations are sometimes connected through source/sink dynamics(56). Jellyfish lost to advection may invade other areas, and immigration in spring from nearby habitats can negate the effect of harsh winters on holoplanktonic jellyfish(12). Coupling several local models similar to the one employed here with a hydrographical model could be used to shed light on such dynamics.

The metagenic jellyfish are dependent on polyps for the spawning of a new adult generation, and limitations to the settlement, survival and growth of polyps can constitute a bottleneck for the adult population (Figure S1). Here we have assumed that the influx of ephyrae in the spring and the previous years' production of planula larvae are independent. Scyphozoan polyps can reproduce asexually, may survive for more than a single season, and often produce more than one ephyrae per season(24). In nature, most of the regulation of ephyrae production is probably acting at the polyp stage and includes predation, density-dependent competition for space, and environmental factors such as temperature(24), and we therefore consider the assumption of independence acceptable, with the caveat that the production of ephyrae fluctuates between years. Riisgård et al.(50) studied populations of *Aurelia* sp. and *M. leidyi* in the semi-enclosed shallow cove of Kertinge Nor, located at the bottom of a fiord. Large numbers of ephyrae (up to 300 ind. M^{-3}) in spring ensured a high abundance of small, food-limited *Aurelia* sp., and whereas *M. leidyi* was present in the outer fiord where *Aurelia* sp. abundances were much lower, the authors concluded that high ephyrae production excluded *M. leidyi* from establishing in the inner part. Similar situations have been observed in Mediterranean French lagoons(51, 52), with similar conclusions.

Here we have examined the interaction between life cycle and environment, and have therefore kept the two jellyfish in our model as equal as possible. For simplicity's sake, we have ignored other important competitors (e.g. fish) and intraguild predation among jellyfish, and we have assumed fixed phenologies of phytoplankton growth and ephyrae production, even though they vary in nature(24). Caveats aside, our study provides insight into mechanisms regulating jellyfish blooms in coastal and semi-enclosed areas, emphasizing particularly how advection and retention should be considered as potentially important for jellyfish population dynamics, and how ephemeral jellyfish blooms can result from environmental noise in combination with jellyfish life history. In addition, we have considered the relative merits of the two contrasting life cycle strategies of jellyfish in a quantitative way, identifying conditions for polyps, seasonal amplitude and year-to-year variation as factors that may shift the relative success of these two strategies.

Jellyfish are not the only planktonic organism group to contain species with either a holoplanktonic or metagenic life cycle. Indeed, metagenic species are common in many plankton groups such as diatoms, dinoflagellates, rotifers and copepods, to name a few(57). The presence of both strategies in many different and diverse groups suggest that these two strategies must have clear and universal trade-offs that are more related to the environment than evolutionary constraints. Our results show how the interaction between life history, seasonality and more irregular environmental fluctuations may govern bloom dynamics and composition of local plankton communities driven by advection, such as in coastal areas or at upwelling sites, and possibly also of communities driven by other environmental variables such as temperature, light or nutrient supply.

We emphasize how theoretical models like the one developed here can provide insight and clarify hypotheses for specific ecological questions, and hopefully inspire other studies to test the predictions and conclusions made here.

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Author contributions

All authors contributed in conceiving the study. N.A.S.-M. performed modelling work, with the help of PM. N.A.S.-M. collected literature references. N.A.S.-M., PM and TK analyzed model output. N.A.S.-M. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Competing Interests

We have no competing interests.

Table 1

Table 1. Metagenic jellyfish abundance $\mathsf{M_a}$***, individual size*** $\mathsf{M_s}$ ***and biomass*** M***, at peak seasonal biomass, for different values of constant water exchange rate*** $\mathbf{\Delta}$***. Simulations run with*** $\mathsf{E} = 20$ ***ind.*** M^{-3}***.***

$\boldsymbol{\Delta}$	M_a (ind. $\mathrm{M^{-3}}$)	M_s (mmol N $\mathrm{ind^{-1}}$)	M (mmol N $\mathrm{m^{-3}}$)
0.01	7.1	0.10	0.74
0.02	2.46	0.26	0.64
0.03	0.95	0.38	0.36

Figure 1

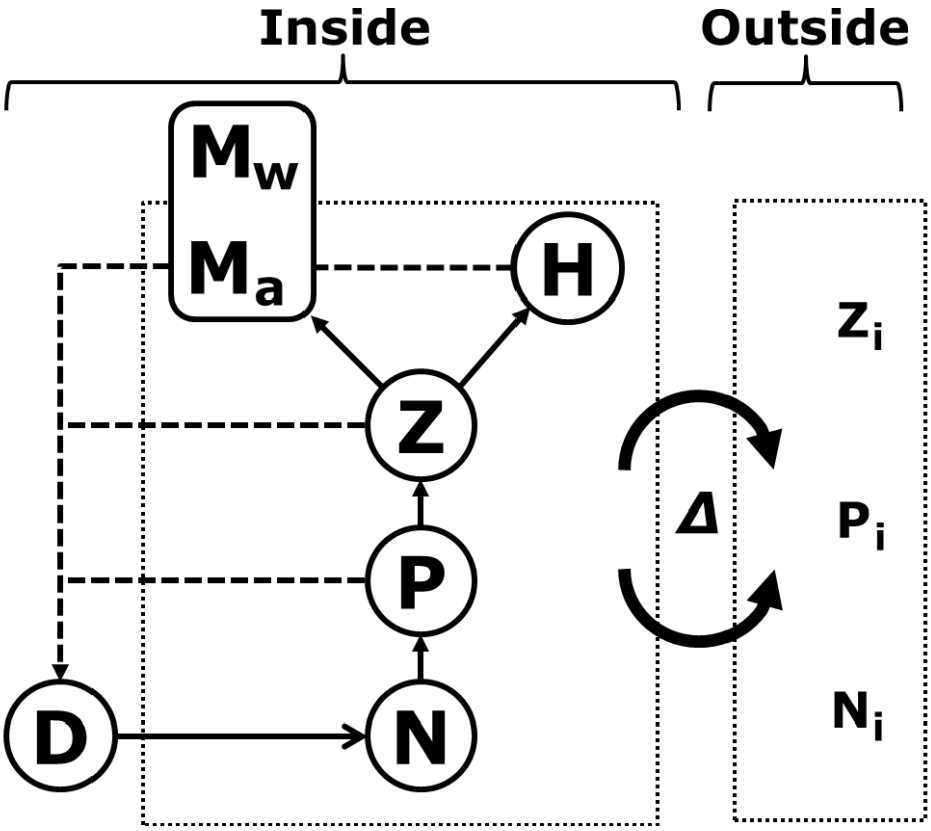


Figure 1. Model system, containing a limiting nutrient (*N*), phytoplankton (*P*), zooplankton (*Z*), detritus (*D*) and two types of jellyfish, holoplantonic (*H*) and metagenic (resolved into individual body mass M_w and abundance M_a). All boxes (except D and M_w) are mixed with water containing outside concentrations of nutrients, phytoplankton and zooplankton (N_i, P_i and Z_i), but no jellyfish, at a water exchange rate Δ.

Figure 2

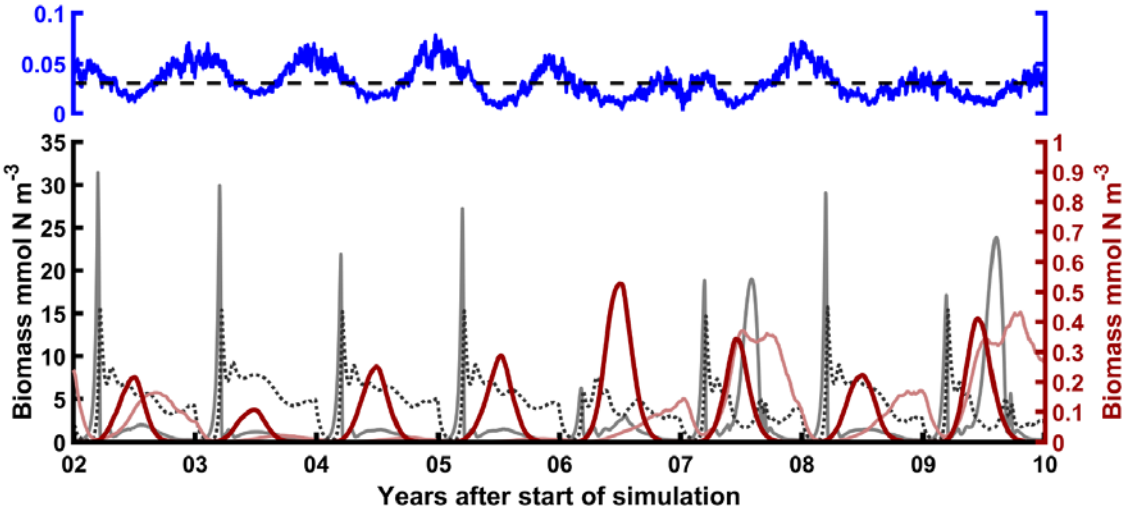


Figure 2. Examples of model predictions using $\mathsf{E} = 20$ ***ind. m^{-3},*** $\bar{\Delta} = 0.03$ ***d^{-1} (dashed line in top axes),*** $\mathsf{A} = 0.5$, ***and*** $\Upsilon = 1$ ***(nutrient and detritus dynamics not shown for clarity). The variability of the environmental forcing (top) drives the interannual variation in the biomasses (bottom). Gray line: Phytoplankton. Black dotted line: Zooplankton. Thick red line: total metagenic jellyfish biomass. Thin pale red line: Holoplanktonic jellyfish. Note the different scales of the bottom y-axes (left: phytoplankton and zooplankton, right: jellyfish).***

Figure 3

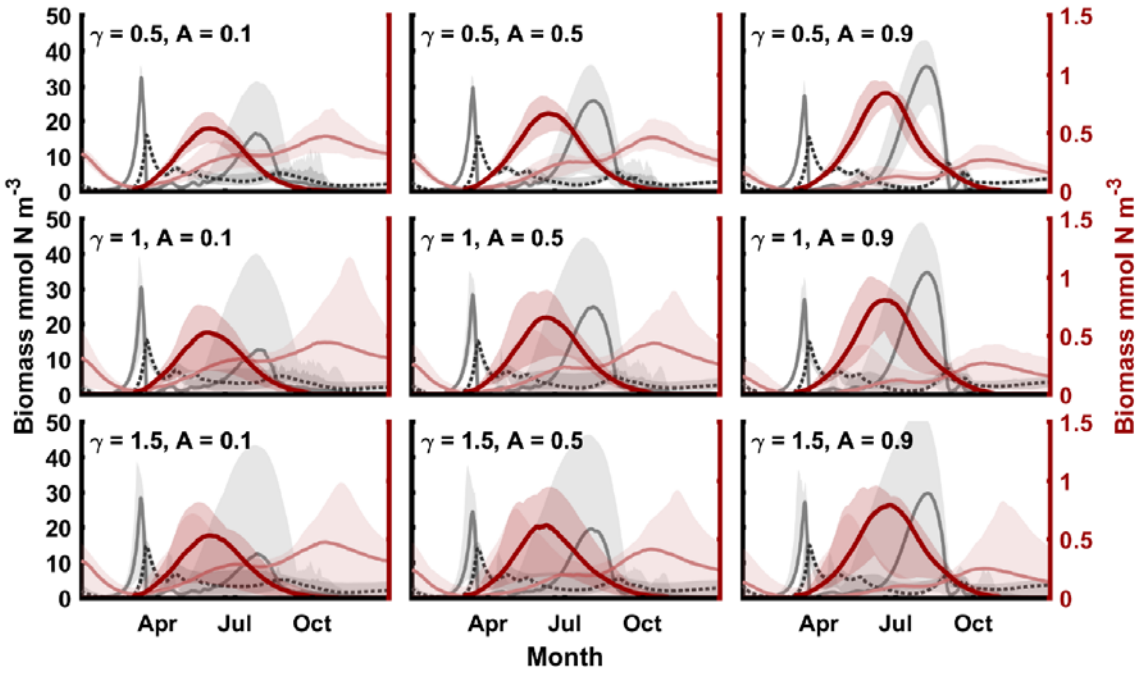


Figure 3. Yearly 'climatologies' of phytoplankton (light grey dashed line), zooplankton (dark grey dotted line), medusa (thick red line) and ctenophore (light red line) mean biomass and variation (100 percent quantiles, shaded areas), for different levels of environmental color (vertical) and seasonal amplitude (horizontal). For all simulations, $E = 20$ ind m^{-3}, and $\bar{\Delta} = 0.025$. ***Note different axis scaling for plankton (left axes in black) and jellyfish (right axes in red).***

Appendix S1: Extended Methods

Model system

We model the seasonal cycle of dissolved inorganic nitrogen N, phytoplankton P, zooplankton Z, detritus D, metagenic jellyfish M and holoplanktonic jellyfish H with the common currency of nitrogen (mmol m^{-3}). The model system interacts with surrounding water masses through a water exchange rate Δ, flushing the system with water containing outside concentrations of nitrogen, phytoplankton and zooplankton, i.e. N_i, P_i and Z_i, respectively, and transporting jellyfish out of the system. Whereas all other populations are described as different state variables and biomasses of nitrogen, metagenic jellyfish biomass is resolved into individual jellyfish nitrogen content (M_w), and abundance (M_a), thus resolving individual and population growth.

The interactions between the model state variables can be written and solved as a set of coupled ordinary differential equations described in the following, and the parameter values can be found in table 1. All model state variables except detritus is subject to overturn through Δ, increasing or decreasing according to the difference between incoming and outgoing concentrations.

The inorganic nitrogen concentration decreases with nutrient uptake by growing phytoplankton, but increases with unassimilated nitrogen from jellyfish ingestion, with jellyfish and zooplankton excretion, and with remineralization of the detritus pool, according to the expression

$$\frac{\partial N}{\partial t} = \Delta(N_i - N) - \mu \frac{N}{K_N+N} P + \left((1-f)\frac{\beta_M Z}{1+h_M\beta_M Z} + r_J\right) M_w M_a + \left((1-f)\frac{\beta_H Z}{1+h_H\beta_H Z} + r_J\right) H + r_Z Z + \rho D \tag{1}$$

where μ is the maximum growth rate of phytoplankton, K_N is the half-saturation constant for nitrogen-limited phytoplankton growth, f is the global assimilation efficiency, β_M and β_H are the specific clearance rates of jellyfish, h_M and h_H are the specific handling times of jellyfish, r_J and r_Z are the jellyfish and zooplankton excretion rates, and ρ is the detritus remineralization rate.

In addition to their dilution and growth, phytoplankton sinks out of the water column with a loss rate s, and is grazed by zooplankton with a type III functional response (FR):

$$\frac{\partial P}{\partial t} = \Delta(P_i - P) + \left(\mu \frac{N}{K_N+N} - s\right) P - \frac{\beta_Z P^2}{1+h_Z\beta_Z P^2} Z \ , \tag{2}$$

where β_M is the specific clearance rate of zooplankton, s is the loss of phytoplankton through sinking and mortality, and h_Z is the specific handling time of zooplankton.

The zooplankton grows with the ingested phytoplankton, and is in turn predated upon by the jellyfish:

$$\frac{\partial Z}{\partial t} = \Delta(Z_i - Z) + \left(f\frac{\beta_Z P^2}{1+h_Z\beta_Z P^2} - \beta_M M_w M_a - \beta_H H - m_Z - r_Z\right)Z \quad (3)$$

where m_Z is the mortality of zooplankton from sources other than predation by jellyfish.

While jellyfish clearance rates are typically constant for (realistic) prey concentrations (e.g. , 28–30), the growth rate does saturate at high prey concentrations, as surplus ingestion is regurgitated (31). Thus the ingestion rate of the two jellyfish in our model follows a type II FR, even if the predation rates in the zooplankton equation follows a type I FR. The rate of change in biomass of holoplanktonic jellyfish increases with prey ingestion, countered by losses though advection, excretion and mortality m_H:

$$\frac{\partial H}{\partial t} = \left(-\Delta + f\frac{\beta_H Z}{1+h_H\beta_H Z} - r_H - m_H\right)H \quad (4)$$

Whereas the populations of the other species in the model are modelled as simple biomasses, the metagenic jellyfish is modelled as two variables, keeping track of both individual size and abundance. A new generation of metagenic jellyfish ephyrae (E, ind. M^{-3}) are released once a year (i.e. March 1st in the model), describing the typical phenology for *Aurelia aurita* (24). This initial abundance (ind. m^{-3}) cannot increase during the course of a season, but only decrease through advection and mortality m_M:

$$\frac{\partial M_a}{\partial t} = -(\Delta + m_M)M_a \quad (5)$$

Any remaining biomass of metagenic jellyfish at the end of the season is moved to the detritus pool (i.e. at November 1st in the model). This resets M_a and M_w to zero in the model, before a new cohort is added the following spring. Conversely, the individual weight of metagenic jellyfish starts at a low value (Mw = 0.0001 mmol N ind.-1, , 58)) each spring, and develops over the season by feeding on zooplankton prey with a given efficiency:

$$\frac{\partial M_w}{\partial t} = \left((1-\vartheta)f\frac{\beta_M Z}{1+h_M\beta_M Z} - r_M\right)M_w \quad (6)$$

where ϑ is the fraction of assimilated prey allocated to reproduction. The factors controlling maturation and reproductive allocation are not very well understood, however, the onset and allocation of resources towards sexual reproduction are plastic with respect to size, and more related to food availability and age (32). In addition Miyake et al. (33) found that gonad maturity of *Aurelia aurita* accelerated with age. This can be described in our model assuming that allocation towards the production of planulae starts at a certain time t_R with a minimum allocation effort that increases linearly as the season progresses:

$$\vartheta = \begin{cases} 0, t < t_R \\ min(\omega, (t - t_R)p), t > t_R \end{cases} \quad (7)$$

where t is the day of the year, ω is the maximum allocation towards reproduction and p is the rate of increase in reproductive allocation (d^{-1}). In the model we set $t_R = 182$, assuming investment in reproduction starts on July 1st. We do not resolve planula settlement and subsequent polyp population dynamics, but rather assume independence between planula and ephyrae production.

At any rate, the vast majority of planulae and polyps will probably perish in the benthos. Consequently, the production of planulae goes into to the detritus pool. Zooplankton non-assimilated prey (fecal pellets), non-ingested jellyfish prey and sinking phytoplankton also go to the detritus pool, which is remineralized into the nitrogen pool with rate ρ:

$$\frac{\partial D}{\partial t} = \left((1-f)\frac{\beta_Z P^2}{1+h_Z\beta_Z P^2} + m_Z\right)Z + \left(\left(\beta_H Z - \frac{\beta_H Z}{1+h_H\beta_H Z}\right) + m_H\right)H + \left(\left(\beta_M Z - \frac{\beta_M Z}{1+h_M\beta_M Z}\right) + \vartheta f \frac{\beta_M Z}{1+h_M\beta_M Z} + m_M\right)M_w M_a + sP - \rho D \quad (8)$$

Seasonal forcing

The seasonal dynamics of the model are forced through seasonal fluctuations of temperature and phytoplankton maximum growth rate:

$$\mu = \frac{\mu_{max}-\mu_{min}}{2}\sin\left(\frac{2\pi}{365}t - \varphi_\mu\right) + \frac{\mu_{max}+\mu_{min}}{2}, \quad (9)$$

where μ_{max} and μ_{min} are the seasonal highest and lowest maximum growth rates of the phytoplankton, and φ_μ is the phase of the growth rate sine function. Likewise, temperature seasonal fluctuation is also a sine curve, with temperature maxima and minima T_{max} and T_{min}, respectively, and phase φ_T:

$$T = \frac{(T_{max} - T_{min})}{2} \sin\left(\frac{2\pi}{365} t - \varphi_T\right) + \frac{T_{max} + T_{min}}{2} \quad (10)$$

Temperature affects physiological variables in the model according to their respective Q_{10} values:

$$k_T = k_{T_{ref}} \times Q_{10.k}^{(T - T_{ref})/10} \ , \quad (11)$$

where k_T, $k_{T_{ref}}$, $Q_{10.ref}$ and T_{ref} are the value at temperature T, reference value, Q_{10} value and reference temperature of parameter k. The parameters that are scaled to temperature are: μ, ρ, r_Z, r_J, β_Z,β_H and β_M.

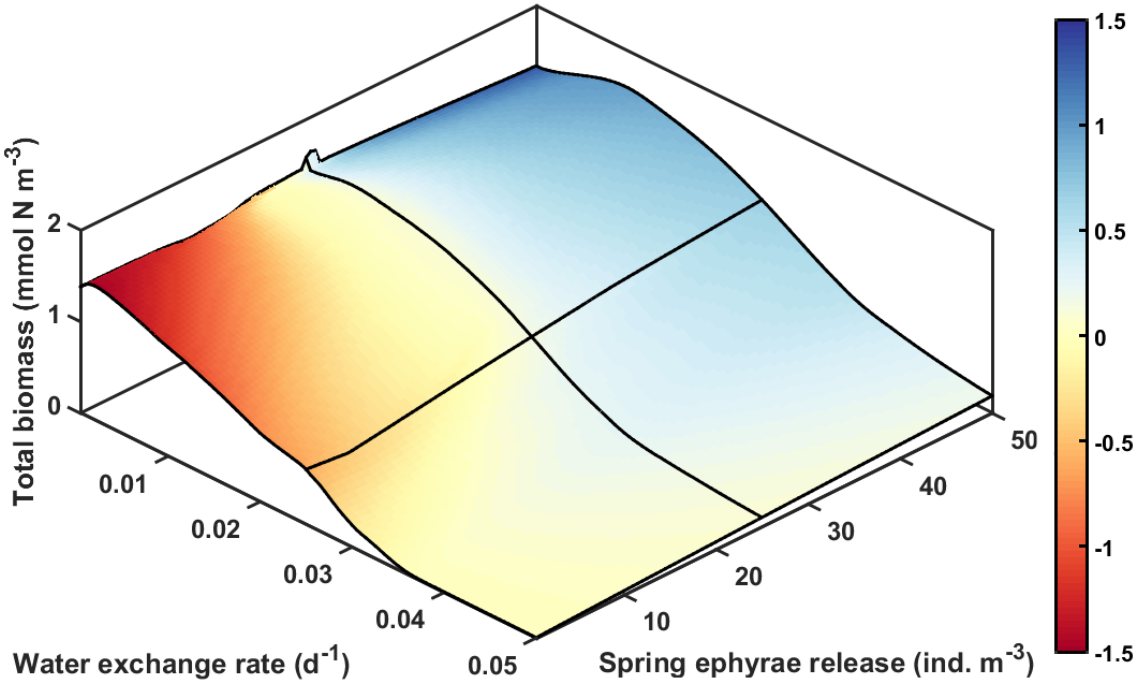
Seasonal concentrations of nitrogen, phytoplankton and zooplankton in the incoming water (N_i, P_i and Z_i) are calculated running the model without jellyfish, null water exchange ($\Delta = 0$), and a total nitrogen pool ($N + P + Z + D$) equal to 70 mmol N m^{-3}. Using these conditions, the model reaches a seasonal with equilibrium with a classical spring phytoplankton bloom, followed by zooplankton increases in summer.

Table A1

Parameter values used in the model.

Symbol:	Value:	Unit:	Note:
μ_{max}	2	d^{-1}	at 20°C.
μ_{min}	0	d^{-1}	-
T_{max}	20	°C	-
T_{min}	1	°C	-
K_N	0.6	mmol N m^{-3}	-
f	0.4	-	-
β_M	-	m^3 d^{-1} mmol N^{-1}	at 15 °C, calculated from size based on Møller and Riisgård (30).
β_H	0.31	m^3 d^{-1} mmol N^{-1}	at 15 °C, calculated based on Møller and Riisgård (30), assuming 0.05 mmol N $ind.^{-1}$.
β_Z	0.28	m^3 d^{-1} mmol N^{-1}	Kiørboe et al. (27).
h_M	-	d	calculated from size and max growth rate, based on Møller and Riisgård (30).
h_H	3.65	d	calculated from size and max growth rate, based on Møller and Riisgård (30), assuming 0.05 mmol N $ind.^{-1}$.
h_Z	1.57	d	Kiørboe et al. (27).
r_J	0.04	d^{-1}	jellyfish excretion rate at 15 °C (59).
r_Z	0.059	d^{-1}	zooplankton excretion rate at 17°C (27).
ρ	0.01	d^{-1}	detritus remineralization rate at 15 °C
s	0.005	d^{-1}	phytoplankton sinking and mortality rate.
m_M	0.005	d^{-1}	-
m_H	0.0125	d^{-1}	-
m_Z	0.005	d^{-1}	-
$Q_{10.P}$	1.88	-	Bissinger et al. (60).
$Q_{10.Z}$	1.8	-	Ikeda et al. (61).
$Q_{10.D}$	2	-	Segschneider and Bendtsen (62).
$Q_{10.J}$	2	-	-
ω	0.8	-	-
p	0.008	d^{-1}	-
φ_μ	1.37	-	-
φ_T	2.1	-	-
φ_Δ	4.8	-	-

Figure A1



Total (z-axis) and difference (color map) of the seasonal peak biomasses of holoplanktonic and metagenic jellyfish, as a function of (constant) water exchange rate Δ, and ephyrae release magnitude E. Total seasonal peak biomass is calculated as the maximum of the summed jellyfish biomasses after April 15th (To avoid dominance of the biomass by the released ephyrae at very low values). The color scale is the difference between the maximum seasonal biomasses of metagenic and holoplanktonic jellyfish, so that positive values indicate dominance of metagenic jellyfish, and negative values indicate holoplanktonic jellyfish.

Chapter 5. **Manuscript III**

Evolution of complex asexual reproductive strategies in jellyfish

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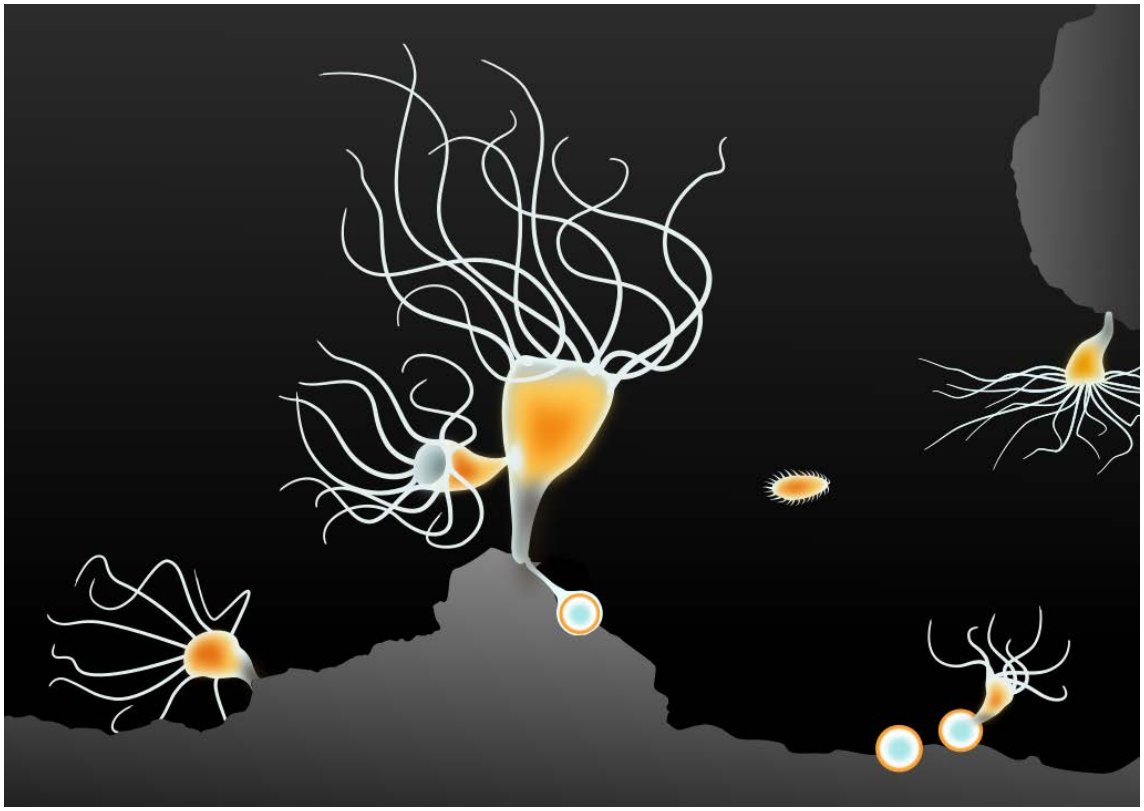

Abstract

Many living organisms in terrestrial and aquatic ecosystems rely on multiple reproductive strategies to reduce the risks of extinction in variable environments. Examples are provided by the polyp stage of several bloom-forming jellyfish species, which can reproduce asexually using different "budding" strategies. These strategies broadly fall into three categories: 1) fast localized reproduction, 2) dormant cysts, or 3) motile and dispersing buds. Similar functional strategies are also present in other groups of species, however, mechanisms leading to the evolution of this rich reproductive diversity are yet to be clarified.

Here we develop an evolutionary model for jellyfish polyps and determine how local population extinction and unequal fitness of the three modes can drive the evolution of multiple reproductive strategies. Depending on environmental parameters, we find that evolution leads to a single evolutionary stable strategy, where in general multiple reproductive modes coexist. As the extinction risk increases, this strategy shifts from pure local budding to a dual strategy, and finally to one characterized by allocation into all three modes. We determine the existence of relative fitness-dependent thresholds in extinction risk where these transitions can occur and we compare our predictions with available literature on polyp reproduction in laboratory and natural systems.

Keywords

Evolutionary stable state, life cycle, dormancy, dispersal, jellyfish polyps, evolutionary model

Introduction:

All ecosystems are subject to changes in the environmental conditions such as repeated natural cycles, episodic events, and long-term trends like climate change. To cope with such spatial and temporal variability, many organisms have evolved strategies that trade off their short-term average fitness in favor of a reduction of risk. These 'bet-hedging' strategies maximize the geometric mean fitness, typically at the expense of a decreasing arithmetic mean fitness [1–3]. Bet-hedging strategies are generally evolutionarily stable strategies (ESSs), and hence non-invasible by rare mutants, because the long-term evolutionary success of a species, genotype or allele is sensitive to rare occurrences of very low fitness or extinction [see e.g. ,4]. In multi-cellular organisms, a classic example of bet-hedging is the evolution of delayed germination (dormancy) or mechanisms of dispersal in the seeds of annual plants [4–7]. Delayed germination and increased dispersal causes the seeds of a single generation to germinate in different years or at different locations, respectively, spreading the risk of low fitness due to adverse conditions. These strategies come at the cost of a reduced fitness in good conditions, because a fraction of propagules do not germinate, or are exported out of the favorable areas, and because of the costs associated with the mechanisms themselves.

In general, the complex interplay between environment and life history traits generates the variety of life history strategies observed in living organisms. However, it remains an open question how and why life history plasticity is maintained in specific groups. An emblematic example is provided by scyphozoan jellyfish. A widely successful and conspicuous animal group, scyphozoans have attracted much attention in the last decades, due to the ability of many species to form large, irregular blooms of their sexually reproducing adults (medusae), with often drastic consequences for ecosystems and human activities [8,9]. The large and conspicuous medusae are typically produced asexually in large numbers by small, inconspicuous and sessile polyps, which are themselves usually capable of multiplying through various modes of asexual budding, and the number of polyps therefore ultimately determines the biomass of adult medusae [10–12]. In recent years, experimental evidence has led to increased knowledge of the propagation strategies available to different species, and to the environmental conditions under which their expression is triggered [11–14]. Reproductive strategy in scyphozoan polyps is extremely plastic: Some species have access to a variety of asexual reproductive modes, while others employ only one or two. It is still unclear, however, exactly what drives this diversity in reproductive modes, and how and under which conditions their various reproductive modes contribute to maintaining polyp populations. Though hypotheses have been put forward about the trade-offs between the three strategies in

multi-modal species [12], we are not aware of an explicit analysis of why similar species of polyps have evolved different combinations of reproductive strategies.

Asexual reproduction in scyphozoan polyps broadly fall into three general modes (see figure 1a) [13,15]: 1) The production of local clones of the parent polyp through budding (hereafter: local budding). The new clone is usually able to start feeding before completion and detachment, making this a very fast reproductive mode under favorable conditions. 2) The production of resting cysts, which are resistant to starvation, predation, and other adverse conditions (up to periods of several years). Cysts require a specific set of environmental conditions to trigger germination, making them the slowest reproductive strategy. 3) The production of (generally smaller) motile and dispersing buds, which do not settle and develop into polyps until after a period of time (days to weeks).

Both in terrestrial and aquatic ecosystems, organisms that can reproduce in several ways, often employ a fast, local asexual reproductive mode in addition to sexual reproduction through smaller, dispersing or dormant propagules. The trade-off between such contrasting modes of reproduction has been studied in the context of sexual vs asexual reproduction [see e.g. ,16] and dispersal vs. vegetative propagation [17]. It is of general interest to investigate trade-offs between dispersal, dormancy and fast local reproduction strategies. From this perspective, scyphozoan polyps are an ideal example of the evolution of reproductive strategy, because of the large variation within the group and because the strategies of dispersal, dormancy and fast local reproduction are embodied within separate reproductive modes in polyps, and not confounded by being traits of the same propagule (as in plant seeds), or by trade-offs between asexual and sexual reproduction.

Here we study the optimal allocation of scyphozoan polyps to the three asexual reproductive strategies under varying parameters, representing environmental conditions. Our aim is to 1) investigate the trade-offs among these three strategies, whether a single optimal strategy exists for a given set of conditions, and under which conditions we can expect coexistence of the three strategies, and 2) to compare model results with the literature on scyphozoan polyp reproduction, and generate further hypotheses about the evolution of reproductive strategies in scyphozoan polyps. To this aim, we introduce a simple evolutionary model, analyzing the emergence of evolutionary stable strategies in the trait space of allocation between the strategies of dispersal, dormancy and rapid local reproduction in a density-dependent metapopulation, evolving in a spatial lattice.

Methods

Competition model

We introduce a metapopulation model describing two competing genotypes (a wild type and a mutant) of a scyphozoan polyp species. The two genotypes occupy an L-by-L square lattice of patches, each representing a suitable local habitat.

In each patch i, the two competing genotypes of polyps can in principle coexist. The local fractions of polyps at generation t belonging to the two types are $N_{i.t}^{w}$ and $N_{i.t}^{m}$. In the first generation (t = 1), the mutant and wild type are present in equal fractions in each patch ($N_{i.1}^{w} = N_{i.1}^{m} = 0.5$ for all i). Both genotypes have access to the three reproductive strategies of local polyps, motile buds, and cysts, but differ in their relative allocation to each strategy. We call f_B the relative allocation to local buds, f_M to motile buds, and f_C to cysts, so that:

Eq. 1. $$f_B^w + f_M^w + f_C^w = 1$$

and similarly for mutants. Apart from this difference in reproductive allocation, the two genotypes are equal. The population dynamics proceed in discrete, non-overlapping generations. We assume that the growth rates are sufficiently large, so that at the end of each generation each patch is either saturated or empty (in the case of a local extinction event, as discussed later). The population density of a saturated patch is conventionally set to one. At each generation and patch, we compute the production of propagules of each of the three types for the two genotypes (figure 1):

- Newborn local buds are simply retained in their local patch and added to the local population of their respective genotype.

- Motile buds are also immediately added to polyp populations, but the production of each individual patch is evenly distributed among itself and the neighboring 8 patches. We assume periodic boundary conditions to avoid border effects.

- Cysts are retained in their local patch, but do not immediately contribute to the polyp population. Instead, they enter the local cyst pool, a fraction h_C of which hatches in each generation.

The number of newborns from each strategy depends on their relative relative fitness. We fix to 1 the reproductive success of local budding, and relative to that for the other

two strategies (r_M for motile buds and r_C for cysts), such that the numbers of newborns in patch i at generation t by local budding, motile bud immigration, and cyst hatching are:

Eq. 2.
$$B_{i.t}^{w} = N_{i.t-1}^{w} f_B^{w} \quad ,$$

$$M_{i.t}^{w} = \sum_{j=1}^{9} \left(\frac{1}{9} N_{j.t-1}^{w} f_M^{w} r_M \right) \quad \text{, and}$$

$$H_{i.t}^{w} = C_{i.t-1}^{w} h_C \quad ,$$

respectively and similarly for mutants**.** Here, j is one of the nine patches (including itself) from which patch i receives immigrants, and $C_{i.t-1}$ is the number of cysts in the cyst pool of patch i at time t-1. The cyst pool increases by the production of cysts, and decreases as cysts hatch, according to:

Eq. 3.
$$C_{i.t}^{w} = C_{i.t-1}^{w}(1 - h_C) + N_{i.t-1}^{w} f_C^{w} r_C$$

In each generation, the contribution of new cysts to the cyst pool is calculated after the number of hatching cysts, to prevent cysts from hatching in the same generation in which they are produced.

The newborns from each reproductive mode are then added together, to form the total number of newborn polyps $S_{i.t}^{w}$ and $S_{i.t}^{m}$ in patch i and generation t, and local competition is implemented by normalizing the final production of polyps of both genotypes, such that $N_{i.t}^{w} + N_{i.t}^{m} = 1$:

Eq. 4.
$$N_{i.t}^{w} = \frac{S_{i.t}^{w}}{S_{i.t}^{w} + S_{i.t}^{m}} \quad \text{, and}$$

$$N_{i.t}^{m} = \frac{S_{i.t}^{m}}{S_{i.t}^{w} + S_{i.t}^{m}}$$

Finally, at the end of each generation, a local extinction can occur with probability e in each patch. In such case, all polyps of both types are killed, i.e. both $N_{i.t}^{wt}$ and $N_{i.t}^{m}$ are set to zero. The patch can then be recolonized from the cyst bank or through immigration of motile buds in the next generation.

Evolutionary model

Our aim is to compare different relative allocation strategies, characterized by their relative allocation to local buds, motile buds and cysts, and look for evolutionary stable strategies (ESSs). ESSs are characterized by not being invasible by a small population of mutants employing any different strategy. To compute ESSs, we use an evolutionary scheme based on random mutation and selection. Starting from a given wild type, we generate a mutation, changing the allocation to reproduction in a random direction such that:

Eq. 5. $$\delta_F = \sqrt{\Delta f_B{}^2 + \Delta f_M{}^2 + \Delta f_C{}^2}$$

where δ_F is the distance between the mutant and the wild type in allocation space. We then simulate the competition model until either the wild type or the mutant reach global extinction.

The surviving genotype becomes the wild type for the next iteration. These dynamics ensures evolution of the wild type towards increased competitive ability. We terminate the evolutionary dynamics once we find a wild type that has not been outcompeted for a number $G_{max} = 40$ of consecutive generations, and we approximate the ESS with such wild type.

Results

Simulations of the competition model always tend to a state where one of the two genotypes outcompetes the other (figure 2a). The values of the parameters used in the models regulate this competitive exclusion. In particular, the difference between growth rates of the two genotypes influences the number of generations needed to reach the equilibrium. Although the system can take many generations to converge, we always observe that the solution is approached without additional transient dynamics.

Letting the wild type evolve according to the evolutionary model, we observe convergence to an ESS characterized by distinct allocations to the three strategies f_B, f_M and f_C (figure 2b).

Importantly, given fixed extinction risk e and relative fitness r_M and r_C, the evolutionary model always converges to the same strategy, independently from the initial distribution of wild and mutant types. This is represented in figure 2c, where strategies are represented as points in relative allocation space, i.e. the triangular surface where Eq. 1 is satisfied and all relative allocations are between zero and one. This indicates that, for a given set of parameters, the evolutionarily stable state (ESS) is unique and

independent of initial conditions. Notice that the evolutionary trajectories show some degree of stochasticity due to the randomness of mutations (figure 2c). Nevertheless, the tracks tend to move in the direction of highest local fitness, thus sketching the portrait of the fitness landscape. For example, when r_M and r_C are similar, the population tends to converge towards the optimal allocation to local buds (f_B), and then motile buds (f_M) and cysts (f_C, see figure 2c). This indicates a higher selection pressure on the fraction of local buds, and a shallower fitness gradient between the fractions of motile buds and cysts. However, when r_M and r_C are different, evolutionary trajectories tend more directly towards the ESS, indicating a more homogeneous fitness gradient around the stable strategy allocation.

Repeating this analysis for different parameter values, we find that both the fitness landscape and the corresponding ESS can change. In particular, the strategy allocation at the ESS is regulated by the extinction risk, and the relative values of r_M and r_C (figure 3). At low extinction risk, local budding is favored, and the ESS is dominated by this strategy at vanishing extinction risk, i.e. $f_B \to 1$, for $e \to 0$. Increasing e, allocation to local budding decreases approximately linearly, and the optimal allocation shifts toward production of cysts and/or motile buds, with $f_B \to 0$, when $e \to 1$. At low or intermediate extinction risk, the ESS is dominated by two strategies: local budding and *either* cysts or motile bud production, except for when their production rates are roughly equal (figure 3). At higher extinction risk, all three reproductive modes do contribute to the ESS, which moves toward relatively similar investment into motile buds and cysts, even when their relative fitness is very different. Finally, at extremely high extinction risks (>0.9), the ESS tends to a pure cyst strategy, except when r_C is zero.

These results are qualitatively robust to changes in other parameters of the model. Similar ESS and evolutionary trajectories are observed at different sums of $r_M + r_C$. The main effect of increasing $r_M + r_C$ is to skew the general pattern in figure 3 away from allocation to local budding. Increasing the hatching rate h_C has the same effect as lowering r_C, meaning that the cysts become more advantageous if they persist in the seed bank for a larger number of generations. We also verified that all these qualitative behaviors are insensitive to lattice size.

Discussion

Evolution of reproductive strategies

We introduced a simple evolutionary model to investigate how and why life history plasticity of scyphozoan jellyfish polyps is maintained in response to variable

environmental conditions. Although the model is developed for jellyfish, it describes the evolution of general reproductive modes, including dispersal (motile buds), dormancy (cysts) and rapid local reproduction (local budding). These strategies are common among both terrestrial and aquatic organisms, hence the results of the model have implications beyond jellyfish ecology. The model predicts an evolutionary stable state characterized by a mixed reproductive strategy for a large range of parameter values. This result appears to be consistent with the presence of multiple reproductive modes in several plants (e.g. [18]), invertebrate (e.g. [19]), and vertebrates (e.g. [20]), as well as other organism groups in aquatic and terrestrial environments.

While coexistence of two or three strategies is a general feature in our model, pure strategies only emerge when the risk of extinctions is negligible (pure local budding strategy) or when the extinction rate approaches the extreme case $e = 1$ (pure cyst strategy). Although in a perfectly risk-free environment rapid reproduction is always superior to other strategies, other strategies can emerge in the presence of local extinctions. This result can be understood in a bet-hedging context, where strategies with lower instantaneous fitness, but which are able to decrease the impact of local extinctions, can invade the system and be transmitted throughout generations. Motile buds and cysts can indeed compensate for the risk of local extinction by spreading the offspring in space and time, although this comes at the cost of a reduced growth rate. This cost is in part due to the lower relative fitness of cysts and motile buds compared to local budding, but also to the fact that some of the motile buds or cysts may end up in regions where extinction does occur. These results reflect studies on reproductive strategies in plants, where traits facilitating dormancy and dispersal in seeds is predicted to be increasingly selected when local extinction rate increases (e.g. [4,5,7], but see also [21]).

Generally, we find that it is the local extinction risk that controls the evolution of the different strategies. At low-to-intermediate extinction risk, dispersal and dormancy strategies are somewhat complementary in our model, and only coexist when their relative fitness is similar. However, when extinction risk is intermediate-to-high, coexistence of both strategies is selected, even when one strategy has a much higher relative fitness. Dormancy and dispersal have similar functional roles, as they both spread the risk of propagules ending up in an unfavorable environment. Many theoretical studies indicate that dormancy and dispersal should evolve to be negatively correlated, consistently with our results at low extinction risk [5,22–24]. However, in the most studied plant systems, dormancy and dispersal are properties of the same seed, where they may interfere with each other or impose different requirements on seed traits [7]. In our model, dispersing motile buds and dormant cysts act independently of one another, only interacting through the trade-off of allocation of limited resources. Contrary to what

has been found before, we observe that increases in the allocation to both reproductive modes at the same time can be adaptive, depending on the level of extinction risk.

Reproduction in jellyfish polyps

Our model predicts that a strategy consisting of more than one reproductive mode should be advantageous in most situations for jellyfish. Similarly, it has been reported that the existence of multiple asexual propagation strategies in the polyps is widespread among scyphozoans [13]. Indeed, many species even have access to several distinct varieties of the three reproductive modes that we considered in this study [12,15]. Species capable of forming blooms are of particular interest due to their conspicuousness and consequences for human well-being, and polyps typically play a large role in bloom formation, because they are the source of the adult generation [11]. Therefore, polyp-to-polyp asexual reproduction has recently begun to attract renewed attention, with experimental studies identifying the reproductive modes available to various species, and in some cases their growth rates and environmental triggers [12–15,25]. Nevertheless, because of the cryptic nature of scyphozoan polyps and the plastic nature of their life history, we do not yet have a clear overview of the distribution and expression of reproductive modes within scyphozoa. It is, however, well known that examples of the three main strategies can be found in all the major branches of scyphozoa [13], and in the following we try to compare our results with the available literature on polyp reproduction.

Given our assumption of higher relative fitness for local budding, we predict that this reproductive mode can dominate the ESS when extinction risk is low. In nature, many of the bloom-forming species have access to local budding [13,26], but, to the best of our knowledge, there are no reported observations of species that have access to local budding only. This is consistent with the model prediction that a pure local budding strategy is evolutionary stable only when $e = 0$, i.e. in the absence of an extinction risk, a condition that can be considered unrealistic in natural environments. Nonetheless, in laboratory experiments where mortality is low and polyps are usually fed ad libitum, species with access to local budding were shown to have much higher reproductive rates compared to those without [12]. Under such conditions, both our results and experimental evidence suggest that species with access to several reproductive modes can allocate 95-100 % of their resources to local budding [12].

According to our model, increased polyp investment into two or more reproductive modes should be a characteristic of more 'risky' environments. High local extinction risk is probably a common occurrence for polyp populations, as jellyfish polyps inhabit frequently disturbed habitats characterized by intense competition for space by other sessile organisms [27]. Moreover, typical predators of jellyfish polyps, like nudibranch mollusks, have very high predation rates on polyps and low mobility, such that they are

patchily distributed but tend to completely clear an area of polyps [28,29]. An example of a jellyfish species commonly employing all three reproductive strategies are the very similar members of the genus *Aurelia*, which are the most frequently blooming jellyfish in the world, with an almost cosmopolitan distribution [9,30,31]. This species most often inhabit variable and changeable estuarine and shallow habitats [32,33,31].

As seen in the data gathered by [13], motile buds are perhaps the least frequent reproductive mode among scyphozoan jellyfish, although their presence might be underrepresented in the literature because it is more cryptic than the two other modes. In the laboratory, both relative and absolute production of motile buds is increased in response to high polyp densities [14]. In an inherently patchy natural environment characterized by high, but spatially uncorrelated extinction risk, occupied and empty habitats will be close to each other, and there will be a large potential for colonization. Our model shows that motile buds could have an important function as dispersers in patchy and ephemeral habitats, supporting long-time survival of the metapopulation besides providing an escape from local density-dependence. Hence we predict that this reproductive mode should be common in such environments; a prediction that can be tested in natural environments.

Cyst production seems to be the most ubiquitous reproductive mode, being present in the majority of species [13]. As expected, cysts are usually produced in response to predation or starvation by species with access to several strategies, although species with access to only cysts production do increase it in response to favorable conditions [11,12,26].

Thus, cysts and motile buds can potentially provide equal, but functionally dissimilar protection against extinctions, as cysts spread extinction risk in time, whereas motile buds spread risk in space. Hence, these two reproductive modes may differ in the type of environmental variation that they most efficiently counter. In the model, we have assumed that extinctions occur randomly, and independently, in both space and time. However, we have also investigated the effect of allowing extinction risk to be increasingly autocorrelated in space, i.e. when extinctions have a large spatial extent compared to the dispersal distance of motile buds (see the Supplementary Information). Under such conditions, when spatial autocorrelation increases, the ESS moves towards increased allocation to cysts. Examples of such events in the real world could be seasonal starvations, or extreme temperature or salinity events, which would be expected to affect a large area at the same time. The common nature of such events in natural (especially seasonal) environments might explain the prevalence of cysts among scyphozoan jellyfish. Here, we have considered long (evolutionary) time scales and, for simplicity, we have assumed that patches are always either full or empty. Neglecting explicit dynamics within a patch is acceptable when the time step is much longer than the characteristic time

scale of growth, which can be very fast in scyphozoan polyps under optimal conditions [14]. However, in nature, the reproductive modes employed by scyphozoans and the extent of their expression can be adjusted in response to e.g. seasonal changes. Although our model lacks an explicit description of the local population dynamics, we expect that our results on the optimal allocation of reproductive strategies should be applicable even when environmental fluctuations on shorter time scales are present.

Future Perspectives

In addition to asexual reproduction, polyp populations in the wild are also at least occasionally reseeded by planula larvae produced by the sexual medusa phase [11]. We speculate that a large and frequent influx of planulae will decrease the advantages of local budding and especially of motile buds, whose primary advantage is the reseeding of empty patches of substrate. In seasonal environments, where the growth rate of polyps can be low and polyps primarily serve as an overwintering stage, this might in part explain why cysts seem to be the most widespread reproductive strategy among scyphozoans [13]. However, as it is not clear what factors governs the trade-off between investment in medusa production and polyp-to-polyp propagation, a model considering the full life cycle including the adult generation is an interesting area for future investigations.

Many marine invertebrates and microorganisms employ some of the strategies discussed here, e.g. the ubiquitous cysts and resting stages of marine plankton [19,34], or the planktonic dispersing larvae of many sessile organisms [35]. However, scyphozoan jellyfish are unique in the richness and complexity of life histories present at all taxonomic levels, and indeed, scyphozoan jellyfish cover much of the spectrum of marine life histories. Scyphozoans are now routinely reared in laboratory cultures [36], facilitating the experimental study of their life histories. We argue that their small size, relative ease of culture, simple bodies and huge reproductive plasticity make scyphozoan polyps an ideal model system for understanding the evolution of life history strategies in the marine environment, and invite experimentalists to test the predictions made here. Our work here represents a first attempt to analyze scyphozoan polyp reproduction in a systematic way, predicting as to the conditions which determine the reproductive modes employed by polyps. We have reduced the diversity of asexual reproductive modes in a way that we believe reflect their functionality instead of physiological detail, and drawn inspiration from the theoretical literature on the evolution of reproductive strategies in plants, which are in many aspects similar to the system we study here. We suggest that this existing theoretical framework represents excellent inspiration for directing research into the intricacies of marine organisms in general, and of scyphozoan jellyfish in particular.

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Figure 1

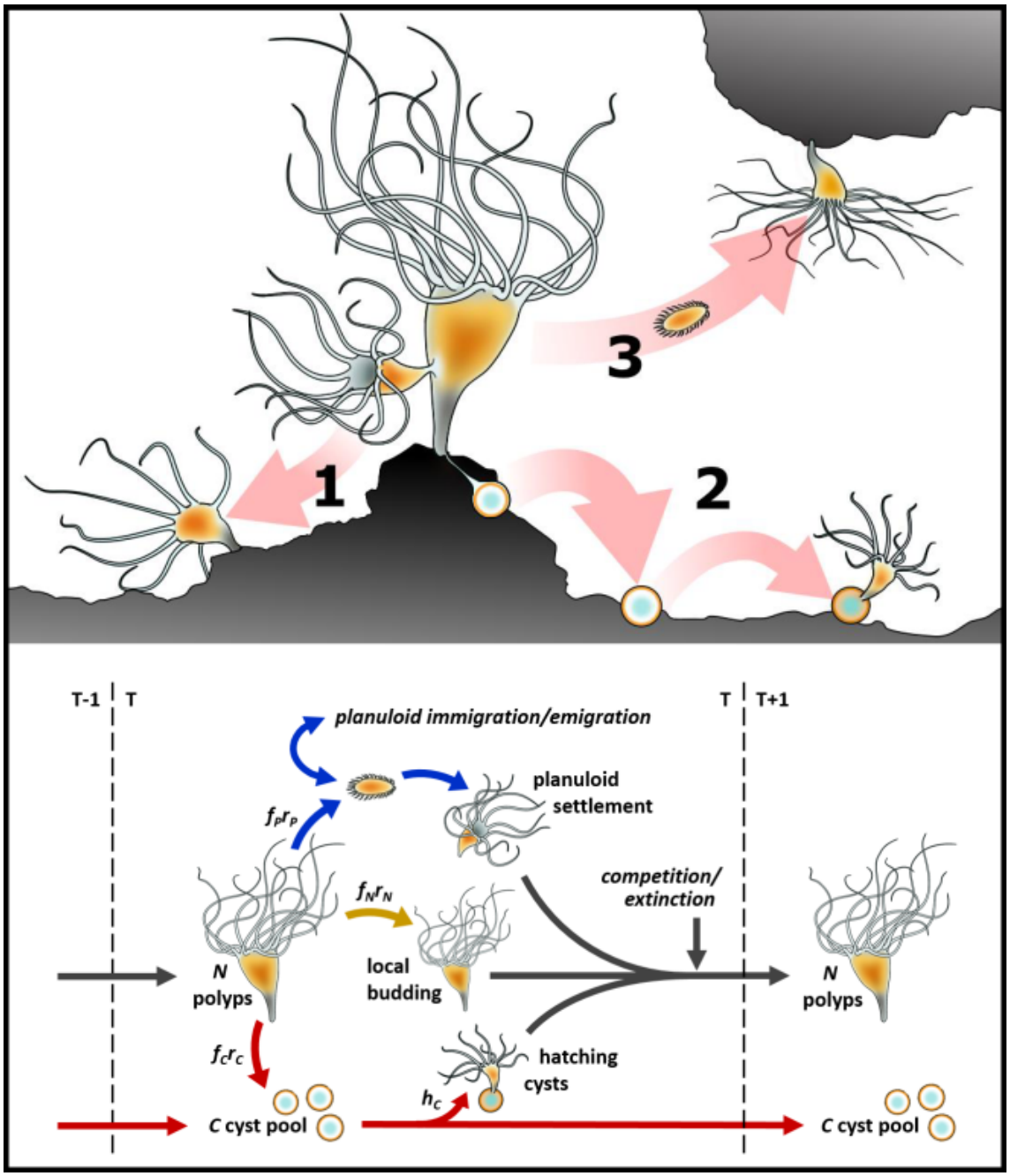

Figure 1. Reproductive strategies and model structure. a) Asexual reproductive modes in scyphozoan polyps fall into three strategies: 1) The budding off of local buds, which are more or less fully developed before detachment. 2) The production of cysts, which are dormant until they hatch into a new polyp at a later time (months-years). 3) The production of motile buds of various types, which go through a dispersing phase before attachment and development. b) Illustration of the model structure in a single patch.

Figure 2

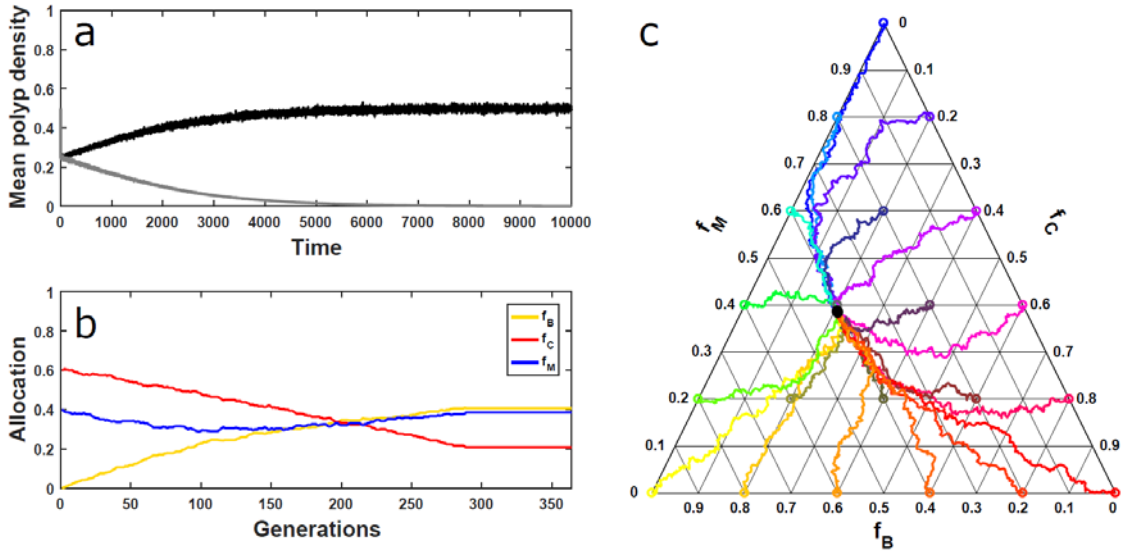

Figure 2. Evolution of life history strategies in the model. a) Competition between a wild type (w, grey) and a mutant (m, black) polyp, leading to competitive exclusion of the wildtype by the mutant. b) Evolution of allocation to the three reproductive strategies through generations of mutation and selection. After ca. 290 generations, the system has reached an evolutionarily stable strategy (ESS). c) Convergent evolution to a common ESS of populations starting with different initial allocation values. For all simulations, parameters are $L = 50$, r_M *and* $r_C = 0.25$, *and* $e = 0.5$.

Figure 3

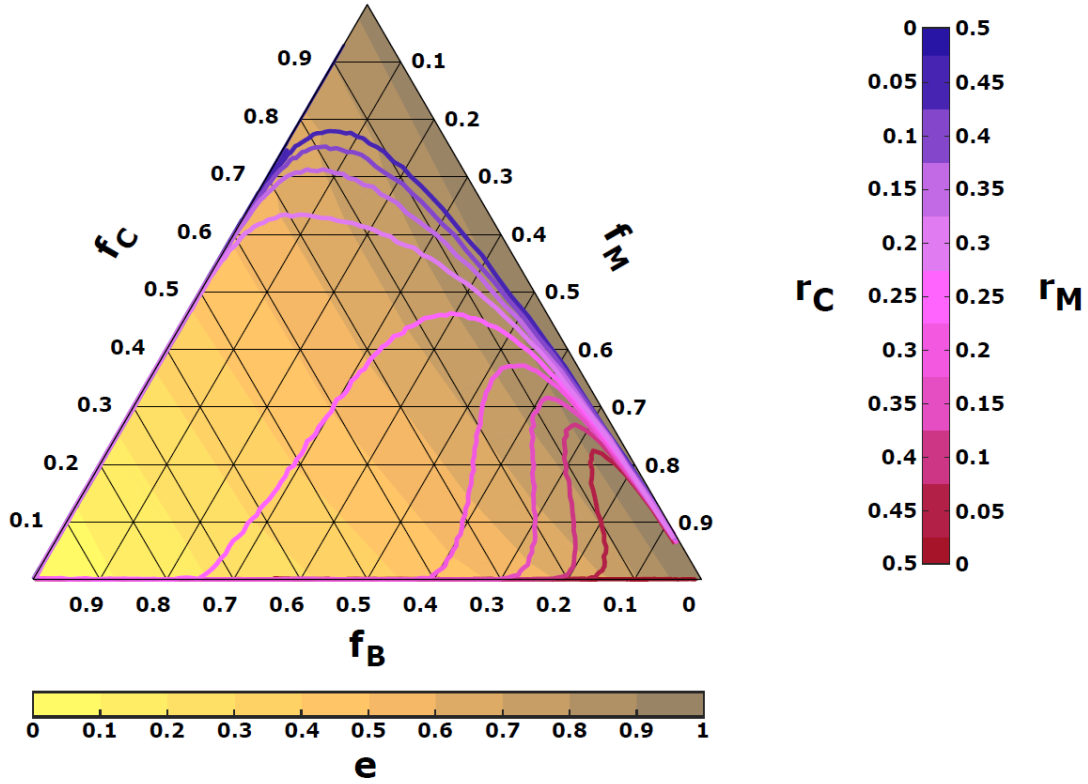

Figure 3. Evolutionary Stable Strategy (ESS), for different parameter choices of relative fitness of motile buds and cysts (r_M and r_C, respectively), and extinction risk e. Lines show the location of the ESS along the gradient of e (shading), for different sets of r_M and r_C, the sum of which is kept constant at a value of $r_M + r_C = 0.5$.

Supplementary Information – spatially correlated extinction risk

Methods

In this Supplementary Information, we investigate the effect of spatially correlated extinction events. To this aim, we introduce a variant of the model, differing in the way in which patches are selected for extinction.

The procedure we implement is the following. At each time step,

1. We assign a random number from the uniform distribution between zero and one to each patch.

2. We then reassign to each patch the average of the random numbers drawn in a square of length r centered on the patch itself.

3. The eL^2 patches with the highest average values undergo extinction events.

With this prescription, increasing the value of r increases the correlation length of extinction events, without changing the number of patches that go extinct which is still set by the parameter e (see figure SI1).

Result

The Evolutionary Stable Strategy (ESS) is affected by spatial correlation (figure SI2). As the value of r increases, the ESS moves towards increased allocation to cysts, mostly at the expense of decreased allocation towards motile buds. Notice that the most radical shift occurs as soon as spatial correlations are introduced, i.e. when moving from $r = 1$ (no spatial correlations) to $r = 3$.

Figure SI1

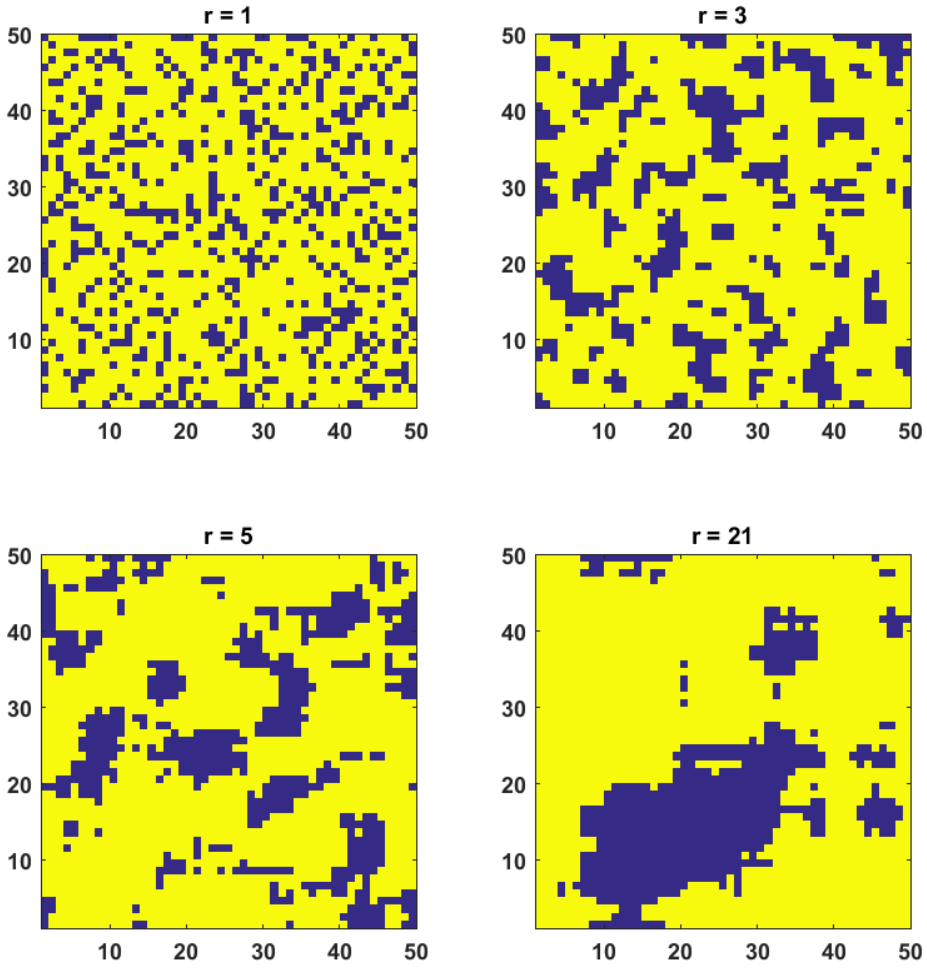

Figure SI4. Spatial patterns of extinctions (blue areas) with increasing r. All panels are with lattice size L = 50, and e = 0.25.

Figure SI2

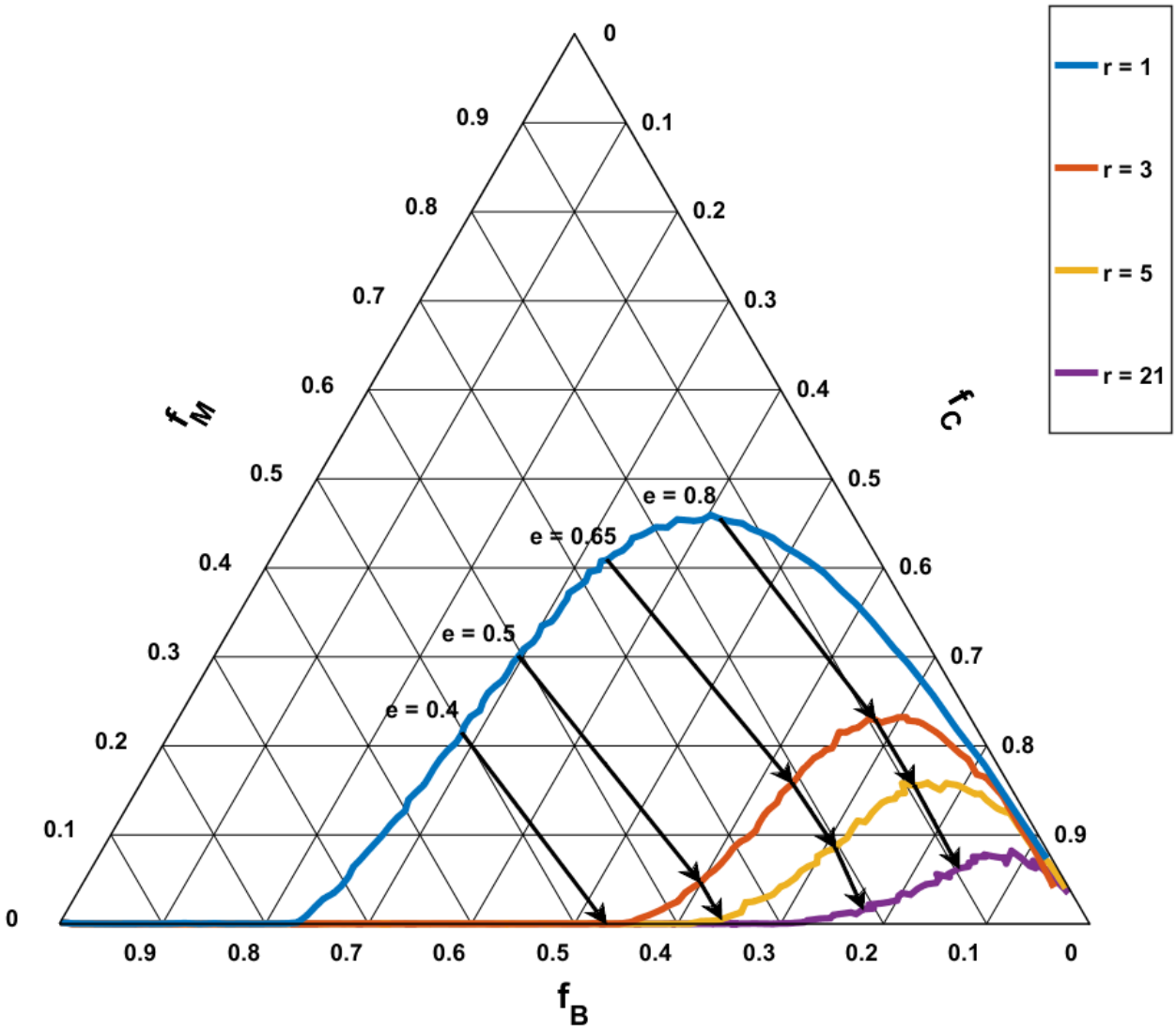

Figure SI5. Evolutionary Stable Strategy (ESS), for different values of r, ***and extinction risk*** e. ***As in figure 3, lines move along a trajectory of increasing extinction risk e. All three lines are with*** $r_M = 0.25$ ***and*** $r_C = 0.25$. ***As spatial correlation increase (increasing*** r***), the ESS moves towards increased allocation to cysts, as shown by the arrows, which are between points with equal extinction risk.***